THE INVERTEBRATE BIODIVERSITY OF DIFFERENTLY AGED ARABLE FARMLAND HEDGEROWS UNDER ENVIRONMENTAL STEWARDSHIP

Sophie Louisa Bennett

A thesis submitted in partial fulfilment of the requirements of the University of Lincoln for the degree of Doctor of Philosophy

July 2016

ACKNOWLEDGEMENTS

With special thanks to my supervisors, Dr Charles Deeming and Dr Paul Eady, who have supported and encouraged me for far longer than they probably anticipated. To Dr Carl Soulsbury for his advice on multivariate analysis also many thanks.

With gratitude to Stewart Watt and the family of FG Battle & Sons for permission to access their hedgerows at Potterhanworth and information so willingly provided on the planting and management of those hedgerows.

Thanks also to Chris Dowse and Malcolm of Sir Richard Sutton's Settled Estates for permission to access hedgerows at Swallow and Dawn and Rose in the Sutton Estates Office for providing me with information and documentation and keeping me abreast of on-farm activities.

Thanks to University of Lincoln colleagues and members of Leverton Farm staff, in particular Terry Metson, for allowing me to work in the hedges/field boundaries of Riseholme Park Farms at both Riseholme and Lodge Farm, Nettleham, and for keeping me informed of activities on the University's farmland, which enabled me to avoid (mostly!) being sprayed or dusted.

To Sally, your advice on formatting was gratefully received – even if I didn't always follow it!

Thank you to the staff of Lincoln County Hospital and Queen's Medical Centre – notably Dr Khalid Hussain, Dr Zuzana Stokes, Caroline Marshall, Mr Adam Brooks and Mr Alex Navarro - whose skill and care following a diagnosis of pancreatic cancer has enabled me to carry on.

Last but not least, I owe my greatest debt of gratitude to my parents, Denise and Roy Bennett. They have sustained me with their love, practical and emotional support, and helped keep me sane-ish throughout, especially during the very difficult period of serious illness which interrupted my work.

ABSTRACT

Hedgerows have been a feature of the British countryside for many centuries and their value to wildlife particularly in farmed areas is long acknowledged. But farmland hedgerows experienced dramatic decline in the 20th century and efforts to halt this decline have been a focal point for agri-environmental activities, with hedge planting and management amongst the most popular options amongst farmers. Despite restoration of many thousands of kilometre of hedgerow under environmental stewardship, the rate of hedgerow loss exceeds the current rate of replacement.

Information regarding the 'performance' of hedgerows as habitat for a range of wildlife is not lacking, although there is less current information regarding the biodiversity of the woody hedgerow itself as opposed to the grassy hedge bottom; I examine both elements of the hedgerow. There is less current information regarding invertebrates than for birds, plants or mammals. A lack of general monitoring has produced a deficit of knowledge of the role farmland hedgerows currently play in maintaining invertebrate biodiversity and what agri-environmental options have achieved.

My objective was to compare and contrast the invertebrate faunas of hedgerows relatively newly-planted under agri-environmental schemes with existing hedgerow stock in order to investigate the biodiversity gains achieved by creation of new habitat. While it was true that overall the diversity of mature hedgerows was greater than that of new hedgerows, for some taxa newer hedges were 'preferred'. There was evidence for the value of even relatively immature (~10 year-old) hedgerow habitats to overall invertebrate diversity.

I did not use a single taxonomic group such as butterflies to 'indicate' diversity, but instead chose to take a view of the broad spectrum of invertebrates collected from both the hedge bottom and hedge top based on higher taxon approaches (notably order), which have been proposed as an adequate means of rapidly assessing the diversity of agricultural land.

A suite of habitat variables including botanical diversity at hedge bottom and top, structural features including the height, width and density of vegetation, as well as weather data were recorded. While weather will always have the ultimate decisive influence on invertebrate activity, structural elements such as the sward height at hedge bottom and the density of the canopy are important to the invertebrate assemblage.

As hedgerow conservation and management become increasingly important in the light of continuing declines, the ability to evidence the effects of interventions efficiently will be crucial. This research underscores the ongoing need for monitoring of hedgerow creation in order to verify whether biodiversity gains are achieved.

PUBLICATIONS

Effect of hedge maturity on composition of invertebrate assemblages at a site in Lincolnshire. D. C. Deeming, S. L. Bennett and C. Morrant (2010). *Aspects of Applied Biology*, 100, 397-403

Invertebrate biodiversity within the grassy and woody elements of farmland hedgerows: snapshots from Lincolnshire. S. L. Bennett, P. E. Eady and D. C. Deeming (2013). *Aspects of Applied Biology*, 118, 253-258

CONTENTS

	ACKNOWLEDGEMENTS		i
	ABSTRACT		ii
	PUBLICATIONS		iii
	LIST OF CHAPTERS		iv-vii
	LIST OF FIGURES		vii-x
	LIST OF TABLES		x-xv
CHAPTER 1. GENERAL INTRODUCTION			**1-14**
	1.1.	The decline of biodiversity and its causes	1
	1.2.	The role of farming in the decline of biodiversity	2
	1.3.	The impact of farming on the diversity of the UK landscape	3
	1.4.	The value of farmland hedgerows as wildlife habitat	5
	1.5.	The benefits of farmland hedgerows to invertebrate diversity	6
	1.6.	Agri-environmental protection of hedgerows	8
	1.7.	Measuring the achievements of AES and hedgerow conservation	10
	1.8.	Evidence for the benefits of AES hedgerow options to invertebrate diversity	11
	1.9.	Hedgerow planting – beneficial effects on invertebrate populations?	12
CHAPTER 2. LITERATURE REVIEW			**15-35**
	2.1.	Introduction	15
	2.2.	Farmland hedgerows as invertebrate habitats – research themes over time	15
		2.2.1. Increasing emphasis on invertebrate diversity	15
		2.2.2. Hedgerow age and invertebrate diversity	19
		2.2.3. The dating of farmland hedgerows	20
		2.2.4. Hedgerow plant diversity and invertebrate diversity	21
		2.2.5. Hedge structure and invertebrate diversity	21
		2.2.6. Evaluation of hedge structure	23
		2.2.7. Hedge management and agri-environment schemes	24
	2.3.	Sampling and surveying techniques for hedgerows	26
		2.3.1. Invertebrate sampling techniques and their effectiveness	26
	2.4.	Measuring invertebrate biodiversity	29
		2.4.1. Invertebrates as bioindicators	29
		2.4.2. Target taxa and taxonomic level for assessment	30
		2.4.3. Use of biodiversity measures	33
CHAPTER 3. GENERAL METHODOLOGY			**36-63**
	3.1.	Hedgerow types	36
	3.2.	Locations and hedge selection	37
	3.3.	Length and location of sampling transect	39
	3.4.	Selection of invertebrate sampling techniques: methods for trapping invertebrates at ground level	40
	3.5.	Sticky trap method for sampling at ground level	42
	3.6.	Selection of invertebrate sampling techniques: methods for collecting invertebrates from the hedge canopy	43
	3.7.	Determining sampling regimen – number of samples	47
	3.8.	Determining sampling regimen - length of trapping session	48
	3.9.	Invertebrate identification and description	48
	3.10.	Measuring invertebrate diversity	49
		3.10.1. Taxon Richness	50
		3.10.2. Berger-Parker index	51
		3.10.3. Shannon diversity index	51
		3.10.4. Simpson diversity index	51

		3.10.5. Heip evenness index	52
		3.10.6. Simpson evenness index	52
	3.11.	Collection of explanatory variables	52
		3.11.1. Landscape context	53
		3.11.1.i. Connectivity	53
		3.11.1.ii. Distance from woodland	53
		3.11.2. Hedge and ground vegetation structure	53
		3.11.2.i. Dimensions of the hedgerow – height, canopy width, height above ground	53
		3.11.2.ii. Dimensions and structure of the margin – margin width, sward height, margin ground cover	54
		3.11.2.iii. Measuring the density of vegetation – canopy light and ground light	54
		3.11.3. Botanical diversity	55
		3.11.3.i. Woody diversity and botanical diversity at ground level	55
		3.11.3.ii. Botanical diversity at trap position	56
		3.11.4. Weather	57
	3.12.	Statistical methods – general overview	57
		3.12.1. Taxonomic abundance distributions	59
		3.12.2. Generalised Linear Model (GLM)	60
		3.12.3. Correlations	61
		3.12.4. Discriminant/Decision Tree Analysis	62
		3.12.5. Taxon Accumulation Curves	62
		3.12.6. Multivariate statistics	62
CHAPTER 4. EFFECTS OF HEDGE AGE ON INVERTEBRATE ASSEMBLAGES AT GROUND LEVEL			**64-117**
	4.1.	Introduction	64
	4.2.	Methods	68
	4.3.	Results	70
		4.3.1. Abundance of invertebrates at ground level/hedge bottom and their taxonomic groups – overview	70
		4.3.2. Effect of time of year and boundary type on the abundance of invertebrates at ground level/hedge bottom	72
		4.3.3. Abundance of individual invertebrate taxa at ground level/ hedge bottom	72
		4.3.4. Total abundance of invertebrates at ground level/hedge bottom	79
		4.3.5. Correlations of invertebrate abundance in the hedge bottom with age of hedgerow in years	82
		4.3.6. Relationships between numbers of individual invertebrate taxa at ground level/hedge bottom	83
		4.3.7. Discriminating between Mature and New hedges using taxonomic abundance at ground level	85
		4.3.8. Comparison of invertebrate taxon accretion of different hedge types/boundaries	86
		4.3.9. Diversity of invertebrates at ground level - effect of hedge/boundary type on diversity indices	87
		4.3.10. Correlations between invertebrate diversity in the hedge bottom and age of hedgerow	92
		4.3.11. Alternative indicators of diversity in the hedge bottom	93
	4.4.	Discussion	95
		4.4.1. Mixed responses of individual taxa to boundary type	97
		4.4.2. Taxa exhibiting greatest abundance in Mature hedges	97
		4.4.3. Taxa exhibiting greatest abundance in New hedges	100
		4.4.4. Taxa exhibiting greatest abundance in Hedgeless boundaries	101

		4.4.5. Taxa for which there was no effect of boundary on abundance	102
		4.4.6. Taxa exhibiting no effect of boundary type or month	106
		4.4.7. 'Rarity' amongst invertebrates at ground level	107
		4.4.8. Response of invertebrate diversity at ground level to boundary type	109
		4.4.9. The use of broad taxonomic groups to assess diversity at ground level	112
		4.4.10. Sticky trapping as a method	114
		4.4.11. Conclusion	116
CHAPTER 5. EFFECTS OF HEDGE AGE ON INVERTEBRATE ASSEMBLAGES OF THE CANOPY			**118-165**
	5.1.	Introduction	118
	5.2	Methods	120
	5.3.	Results	121
		5.3.1. Abundance of hedge canopy invertebrates and their taxonomic groupings	121
		5.3.2. Effect of hedge type and month on invertebrate abundance at canopy level	123
		5.3.3. Correlations of canopy-active invertebrate abundance with age of hedgerow in years	132
		5.3.4. Relationships between individual invertebrate taxa in the hedge top	133
		5.3.5. Discriminating between hedge types (Mature versus New) using taxonomic abundance in the canopy	135
		5.3.6. Diversity of canopy invertebrates – hedge age and taxon accretion rates	137
		5.3.7. Effect of time of year and boundary type on the diversity indices of canopy invertebrates	137
		5.3.8. Correlations between canopy invertebrate diversity with age of hedgerow	138
		5.3.9. Alternative indicators of invertebrate diversity in the hedge canopy	142
	5.4.	Discussion	144
		5.4.1. Mixed responses to hedge age by canopy invertebrates	144
		5.4.2. Invertebrates of hedgerow canopies – a neglected theme?	145
		5.4.3. Taxa exhibiting greater abundance in Mature hedge canopies	147
		5.4.4. Taxa exhibiting greater abundance in New hedges	149
		5.4.5. Taxa exhibiting effect of month but no effect of hedge type on abundance	149
		5.4.6. Taxa exhibiting no effect of hedge type or month	157
		5.4.7. 'Rarity' amongst canopy invertebrates	158
		5.4.8. Invertebrate diversity in the hedge canopy	160
		5.4.9. The use of broad taxonomic groups in assessing diversity of the canopy	162
		5.4.10. Beating as a sampling technique	163
		5.4.11. Conclusion	164
CHAPTER 6. DETERMINANTS OF HEDGEROW INVERTEBRATE ASSEMBLAGES			**166-224**
	6.1.	Introduction	166
	6.2.	Methods	170
		6.2.1. Collected variables	170
		6.2.2. Statistical analysis	172
	6.3.	Results	174
		6.3.1. Botanical diversity – effects on invertebrate abundance and diversity	174
		6.3.1.i. Invertebrate abundance	175
		6.3.1.ii. Invertebrate diversity	176
		6.3.2. Ground vegetation structure – effects on invertebrate abundance and diversity	177

		6.3.2.i. Invertebrate abundance	180
		6.3.2.ii. Invertebrate diversity	182
		6.3.3. Hedge Structure – effects on invertebrate abundance and diversity	188
		6.3.3.i. Invertebrate abundance	188
		6.3.3.ii. Invertebrate diversity	190
		6.3.4. Landscape context – effects on invertebrate abundance and diversity	196
		6.3.4.i. Invertebrate abundance	196
		6.3.4.ii. Invertebrate diversity	197
		6.3.5. Weather – effects on invertebrate abundance and diversity	202
		6.3.5.i. Invertebrate abundance	203
		6.3.5.ii. Invertebrate diversity	204
	6.4.	Discussion	210
		6.4.1. Botanical diversity	210
		6.4.2. Ground vegetation structure	213
		6.4.3. Hedge structure	215
		6.4.4. Landscape context	218
		6.4.5. Weather	220
		6.4.6. Conclusion	222
CHAPTER 7. GENERAL DISCUSSION AND CONCLUSIONS			**225-241**
	7.1.	Effects of hedgerow maturity on the invertebrate assemblage	225
		7.1.1. Effects of hedgerow maturity on invertebrate abundance	225
		7.1.2. Effects of hedgerow maturity on invertebrate diversity	227
	7.2.	Relationships with other studies on effects of habitat restoration/maturity	228
	7.3.	The influence of seasonality	230
	7.4.	Other key factors affecting the invertebrate assemblage	231
	7.5.	Utility of a higher taxon approach to measure invertebrate diversity	234
	7.6.	Use of sampling methods	237
	7.7.	Use of diversity indices	238
	7.8.	The future of farmland hedgerows	239
	7.9.	Concluding comments on AES hedge planting and invertebrate assemblages	240
REFERENCES			**242-264**
APPENDICES (on CD)			**265-350**
	Appendix A. Supplementary information relating to Chapter 3		**265-280**
	Appendix B. Supplementary information relating to Chapter 4		**281-308**
	Appendix C. Supplementary information relating to Chapter 5		**309-329**
	Appendix D. Supplementary information relating to Chapter 6		**330-350**
LIST OF FIGURES			
	Figure 2.1. Annual number of published items 1985 - 2015 for the search terms "hedgerow*" AND (UK OR United Kingdom OR GB OR Great Britain OR England) as topics. Source: Thomson Reuters™ Web of Science™. Correct 01 February 2016		17
	Figure 2.2. Annual number of published items 1985 – 2015 for the search terms "hedgerow*" AND (invertebrate* OR insect* OR arthropod*) AND (diversity OR biodiversity) AND (UK OR GB OR Great Britain OR United Kingdom OR England) as topics. Source: Thomson Reuters™ Web of Science™. Correct 01 February 2016		17
	Figure 3.1. Comparison of basic structure of Mature and New hedgerows (photographic examples from University of Lincoln farmland). A Mature hedge is shown on the left and a 'New' hedge on the right complete with white tree guards. The vertical yellow stick measures one metre. This is for illustrative purposes only, as not all hedgerows conformed to these dimensions		38

	Figure 3.2. Schematic diagram of the cross-section of a hedgerow. A vertical line marks the centre of the hedgerow, and the 'protection zone'/margin is shown in profile. The minimum requirements for hedge height are shown and the main hedgerow options for Entry Level Stewardship are indicated: EB1 = management on both sides of the hedge, EB2 = management on one side of hedge, EB3 = Hedgerow management for landscape and wildlife. Source: Natural England, 2010. © Natural England/Charlotte Lemmon	39
	Figure 3.3. Schematic diagram of the cross-section of a hedgerow, showing the 2 metre protection zone which must be protected from incursion and pollution under basic Cross compliance (GAEC 14). Source: RPA, 2011. ©Richard Yardley, Natural England	39
	Figure 3.4a-f. Photographs of sticky trap and protective cage, showing: (a) Cockroach trap sticky pad cut to size; (b) sticky pad on adapted demi diamond moth trap holder (manufactured by Killgerm); (c) demi diamond holder with sticky pad closed; (d) wire mesh (6mm x 6mm gauge) protective cage, viewed from narrow end; (e) wire mesh protective cage containing sticky trap seen from above, open at one end; (f) protective cage containing sticky trap seen from above, closed and ready for setting. Garden wire (green) securing cage in a closed position can be seen	44
	Figure 3.5. Sticky trap in protective cage in situ in the field at hedge bottom April 2011	45
	Figure 3.6a-b. Photographs of sticky traps illustrating catches: (a) sticky pad from September 2011, highlighting larger Carabid beetle (circled in red on the right) and smaller Carabid (circled in red on the left). Sample is characterised by numerous Opiliones (harvestmen); (b) sticky pad from July 2011 showing range and distribution of animals caught, including Diptera, Hemiptera (notably Leafhoppers), small Hymenoptera (Parasitica) and Isopoda	45
	Figure 3.7. Demonstration of a conventional beating technique showing a beating tray being held up beneath a bush and the collector holding a beating stick. Source: WSU Pest Management Transition Project, http://appleipm.blogspot.co.uk/2011/05/western-flower-thrips-campylomma-in.html	45
	Figure 3.8a-b. Beating funnel illustrating both (a) the original 28cm diameter plastic food funnel, and (b) the enlarged 50cm diameter funnel incorporating dog collar. Collecting containers are also shown	45
	Figure 3.9. Investigator demonstrating the adapted beating technique using 50cm diameter funnel (with collecting container) to sample invertebrates from a domestic Common Hawthorn (*Cretaegus monogyna*) hedge	45
	Figure 3.10. Invertebrate taxon (order/class) accretion for the hedgerow with lowest taxon richness showing mean (±SE) cumulative number of taxa collected on the y-axis and cumulative number of traps on the x-axis. Invertebrates collected by pitfall trapping in April 2007	50
	Figure 3.11. Accretion rate of invertebrate taxon richness (± SE) over time for sticky trapping sessions of different durations, comparing one Mature (~100 years) and one New (~5 years) hedge. The y-axis shows mean number of taxa per sticky trap (n = 5). The y-axis shows the trapping session durations (2, 3, 4, 5 days respectively)	50
	Figure 3.12. Locating the botanical survey quadrats within the survey transects at ground level following the Hedgerow Survey Handbook method. Source: Defra, 2007. © Crown Copyright 2007	56
	Figure 3.13. Position of ground flora survey quadrats (2m x 1m) in the hedge. Reproduced from the Hedgerow Survey Handbook. Source: Defra, 2007. © Crown Copyright 2007	57
	Figure 4.1. Taxonomic Abundance Distribution plots for invertebrates collected from hedge bases in 2011: (a) April; (b) July; (c) September. Line plots show mean number of organisms per hedge/boundary against taxonomic rank (most to least abundant) for all boundary types (Mature hedges, New hedges and Hedgeless boundaries)	73

	Figure 4.2a-h. Mean abundance (± SE) per hedge/boundary of invertebrates collected by sticky trap at ground level, shown by boundary type (Mature hedges, New hedges, Hedgeless boundaries) and month (April, July, September) in 2011: (a) Collembola; (b) Hymenoptera; (c) Acari; (d) Hemiptera; (e) Diptera; (f) Opiliones; (g) Thysanoptera; (h) Coleoptera	80
	Figure 4.2i-p. Mean abundance (± SE) per hedge/boundary of invertebrates collected by sticky trap at ground level, shown by boundary type (Mature hedges, New hedges, Hedgeless boundaries) and month (April, July, September) in 2011: (i) Araneae; (j) Isopoda; (k) Dermaptera; (l) Lepidoptera; (m) Julida; (n) Psocoptera; (o) Pulmonata; (p) Siphonaptera	81
	Figure 4.3. Mean abundance (± SE) of all ground-occurring invertebrates (combined) per boundary for each boundary type: Mature hedges (n = 16), New hedges (n = 16), Hedgeless boundaries (n = 4). Invertebrates collected during April, July and September 2011 using sticky traps	82
	Figure 4.4a-c. Taxon accretion curves showing the cumulative number of ground-occurring invertebrate taxa recovered with increasing number of hedges/boundaries sampled for: (a) April; (b) July; (c) September. Boundary types are: Mature Hedges (n = 16) and New Hedges (n = 16 in April & July, n = 15 in Sept). Vertical lines are ± SE	89
	Figure 4.5a-f. Box and whisker chart showing the median (♦), inter-quartile range (shaded box), maximum and minimum values (represented by caps on whiskers above and below box) for each month (April, July, September) and boundary type (Mature hedges, New hedges and Hedgeless boundaries) for the following measures of diversity: (a) taxonomic richness; (b) Berger-Parker (*d*); (c) Shannon indices (*H*'); (d) Heip evenness (E_{Heip}): (e) Simpson diversity (reciprocal – 1/D); (f) Simpson evenness ($E_{1/D}$)	91
	Figure 5.1. Mean abundance (± SE) of all taxa collected by beating, per boundary type (Mature hedges and New hedges) per month (April, July, September) in 2011	121
	Figure 5.2a-c. Taxonomic Abundance Distribution curves for canopy-active invertebrates collected in: (a) April; (b) July; (c) September. Line plots show mean number of organisms per hedge against taxonomic rank (most to least abundant) for both Mature and New hedges	125
	Figure 5.3a-h. Mean abundance (± SE) of taxa collected by beating, per boundary type (Mature hedges and New hedges) per month (April, July, September) in 2011: (a) Collembola; (b) Coleoptera; (c) Hemiptera; (d) Araneae; (e) Acari; (f) Hymenoptera; (g) Thysanoptera; (h) Psocoptera	128
	Figure 5.3i-m. Mean abundance (± SE) of taxa collected by beating, per boundary type (Mature hedges and New hedges) per month (April, July, September) in 2011: (i) Diptera; (j) Lepidoptera; (k) Pulmonata; (l) Dermaptera; (m) Opiliones	129
	Figure 5.4a-c. Taxon accretion curves, showing the cumulative number of invertebrate taxa collected from Mature and New hedge canopies as sampling increased. Curves are shown for each month: (a) April; (b) July; (c) September. Vertical lines are ± SE	139
	Figure 5.5 a-f. Box and whisker chart showing the median (♦), inter-quartile range (shaded box), maximum and minimum values (represented by caps on whiskers above and below box) for each month (April, July, September) and hedge type (Mature hedge, New hedge) for: (a) Taxon Richness; (b) Berger-Parker; (c) Shannon; (d) Heip; (e) Simpson (diversity); (f) Simpson (evenness)	141
	Figure 6.1a-b. Summed candidate Akaike model weights for botanical diversity variables potentially explaining invertebrate abundance at: (a) ground level, and (b) canopy level. Top 10 most abundant taxa only are shown for hedge bottom and hedge top respectively, as well as Total abundance (all taxa). Key to explanatory variables: WTR = Woody taxon richness in the hedgerow itself; MVTRQ = Botanical taxon richness in the margin; TVTR = taxon richness of vegetation in immediate vicinity of trap	180

	Figure 6.2a-b. Summed Akaike model weights for structural measures of ground vegetation potentially explaining invertebrate abundance at: (a) ground level, and (b) canopy level. Top 10 most abundant taxa only are shown for hedge bottom and hedge top respectively, as well as Total abundance (all taxa). Explanatory variables: Ground Cover; Ground Light; Max sward (height); Margin Width	185
	Figure 6.3a-b. Summed Akaike model weights for structural elements of ground vegetation potentially explaining measures of invertebrate diversity (Taxon Richness, Berger-Parker, Shannon, Simpson, Heip, Simpson Evenness) at: (a) ground level, and (b) canopy level. Explanatory variables: Ground Cover; Ground Light; Max Sward (height); Margin Width	185
	Figure 6.4a-b. Summed Akaike full model weights for measures of hedge structure potentially explaining invertebrate abundance at: (a) ground level, and (b) canopy level. Top ten most abundant taxa at hedge bottom and hedge canopy are shown, as well as Total abundance (all taxa). Variables: Canopy Light; Height Above Ground; Width Growth; Width; Height Growth; Height	193
	Figure 6.5a-b. Summed Akaike full model weights for aspects of hedge structure potentially explaining measures of invertebrate diversity (Taxon Richness, Berger-Parker, Shannon, Simpson, Heip, Simpson Evenness) at: (a) ground level, and (b) canopy level. Variables: Canopy Light; Height Above Ground; Width Growth; Width; Height Growth; Height	193
	Figure 6.6a-b. Summed Akaike model weights for measures of landscape context potentially explaining invertebrate abundance at: (a) ground level, and (b) canopy level. Total abundance and top ten most abundant taxa at hedge bottom and hedge canopy are shown. Variables: Connectivity; Location; Distance from Woodland	201
	Figure 6.7a-b. Summed Akaike model weights for measures of landscape context potentially explaining measures of invertebrate diversity (Taxon Richness, Berger-Parker, Shannon, Simpson, Heip, Simpson Evenness) at: (a) ground level, and (b) canopy level. Variables: Connectivity; Location; Distance from Woodland	201
	Figure 6.8a-b. Summed Akaike model weights for weather variables potentially explaining invertebrate abundance at: (a) ground level, and (b) canopy level. Top ten most abundant taxa at hedge bottom and hedge canopy are shown, as well as the Total abundance for all taxa combined. Explanatory variables: Rain; Wind speed; Humidity; Temperature	207
	Figure 6.9a-b. Summed Akaike model weights for weather variables potentially explaining invertebrate diversity (Taxon Richness, Berger-Parker, Shannon, Simpson, Heip, Simpson Evenness) at: (a) ground level, and (b) canopy level. All months combined: April, July, September. Explanatory variables: Rain; Wind speed; Humidity; Temperature	207
LIST OF TABLES		
	Table 4.1. Taxonomic rank showing total abundance of invertebrates for individual taxa ranked from most to least abundant. Totals for each month (April, July, September) and a grand total for All months and All boundaries (Mature hedges, New hedges and Hedgeless boundaries combined) are shown. Invertebrates collected from sticky traps at ground level	71
	Table 4.2. Results of a ranked ANCOVA (Quade procedure) and LSD post hoc multiple comparisons of taxonomic abundance distributions for each boundary type (Mature hedges, New hedges and Hedgeless boundaries) and month of sampling (April, July and September)	72
	Table 4.3. Results of a Generalised Linear Model (GLM) analysis of the abundance of all invertebrate taxa collected by sticky trap from the hedge bottom, comparing the effect of time (Month: April, July, September) and habitat (Boundary type: Mature hedges, New hedges and Hedgeless boundaries). Values are Wald χ^2 plus significance values	75

	Table 4.4. Results of a Generalised Linear Model analysis of the effects of month (April, July, September) and boundary type (Mature hedge, New hedge, Hedgeless boundary) on the total abundance of all invertebrate taxa collected by sticky trapping at ground level	82
	Table 4.5. Spearman's ranked pairwise correlations between the abundance of invertebrate taxa sticky trapped in the hedge bottom: all months combined, all boundaries (n = 107). Top 5 correlates (Acari, Araneae, Hemiptera, Hymenoptera, Thysanoptera) only shown. Values are r_s plus significance values. Significant values are highlighted in bold. A Benjamini –Yekultieli method FDR corrected significance level of 0.008 applies	84
	Table 4.6. Spearman's ranked pairwise correlations between the abundance of invertebrate taxa sticky trapped in the hedge bottom: all months combined, hedges only (n = 95). Top 3 correlates (Acari, Hymenoptera, Thysanoptera) only shown. Values are r_s plus significance values. Significant values are highlighted in bold. A Benjamini –Yekultieli method FDR corrected significance level of 0.008 applies	84
	Table 4.7. Results of a Generalised Linear Model (GLM) analysis of the invertebrate diversity of organisms collected by sticky trap from the hedge bottom, comparing the effect of time (Month: April, July, September) and habitat (Boundary type: Mature hedges, n = 16; New hedges, n = 16*; Hedgeless boundaries, n = 4). Values are Wald χ^2 plus significance values	90
	Table 4.8. Spearman's rank correlations between abundance of taxonomic groups and diversity measures. Top 5 correlates only shown: Collembola, Hemiptera, Hymenoptera (all), Hymenoptera (Parasitica) and Opiliones. All hedges/boundaries combined for all months combined (n = 107). The B-Y FDR corrected significance level of 0.010 applies	94
	Table 4.9. Total number of superfamilies/families of Coleoptera and Diptera identified in Mature Hedges (n = 16), New Hedges (n = 16) and Hedgeless boundaries (n = 4) for April, July, September. Abbreviations: M = Mature hedge, N = New hedge, H = Hedgeless	94
	Table 5.1. Results of a Generalised Linear Model analysis of the effects of month (April, July, September) and hedge type (Mature hedges, New hedges) on the total abundance of all invertebrate taxa	122
	Table 5.2. Results of a ranked ANCOVA (Quade procedure) comparing taxonomic abundance distributions (TADs) of Mature hedges and New hedges for each month of sampling (April, July and September)	125
	Table 5.3. Taxonomic rank showing total abundance of canopy invertebrates for individual taxa ranked from most to least abundant. Totals for each month (April, July, September) and a grand total for All months and both boundary types (Mature hedges and New hedges) combined	126
	Table 5.4. Results of a Generalised Linear Model (GLM) analysis of the abundance of all invertebrate taxa collected through beating from the hedge canopies. The effect of time (Month: April, July, September) and habitat (Mature hedges versus New hedges) is compared. Values are Wald χ^2 plus significance values. Significant values are highlighted in bold	127
	Table 5.5. Correlations between abundances of canopy-active taxa for all hedgerows (Mature and New) combined (n = 83) and all months combined (April, July, September). Top 3 correlates only shown: Collembola, Hemiptera, Hymenoptera. A corrected significance level of 0.009 applies	134
	Table 5.6. Results of a Generalised Linear Model (GLM) analysis of the canopy-active invertebrate diversity of organisms collected by beating, comparing the effect of time (Month: April, July, September) and habitat (Boundary type: Mature hedges and New hedges) Values are Wald χ^2 plus significance values. Significant values at the $p = 0.05$ level are highlighted in bold	140

	Table 5.7. Results of Spearman's *rho* correlations between hedgerow age (years) and canopy-active invertebrate diversity for all months combined and individually (April, July and September) for New hedges only. Values are r_s plus significance values. Significant values are highlighted in bold. An FDR (Benjamini and Yekuelti) corrected significance level of 0.018 was applied	140
	Table 5.8. Spearman's rank correlations between abundance of Coleoptera and Psocoptera and diversity (Taxon Richness, Berger-Parker, Shannon, Simpson (diversity), Heip, Simpson (evenness)) of the hedge canopy for Mature hedges and New hedges, all months combined (n = 83)	143
	Table 5.9. Total number of superfamilies/families of Coleoptera and Diptera identified from Mature hedge canopies, New hedge canopies for April (n = 13 per hedge type), July (n = 16), September (n = 13). Abbreviations: M = Mature hedge, N = New hedge, H = Hedgeless	143
	Table 6.1. Abbreviations and definitions of biotic and abiotic variables used in statistical analysis explaining hedgerow invertebrate abundance and diversity	171
	Table 6.2. Best models ($\Delta i \leq 2$) predicting the abundance of invertebrate taxa in hedgerows at ground level (upper table) and canopy level (lower table), using measures of botanical diversity as explanatory variables. Explanatory variables: WTR = Woody taxon richness in the hedgerow itself; MVTRQ = Botanical taxon richness in the margin; TVTR = taxon richness of vegetation in immediate vicinity of trap. Total abundance (all taxa) only shown	178
	Table 6.3. Comparison of the averaged full-model Akaike weightings for each measure of botanical diversity used as explanatory variables for invertebrate abundance (all taxa and top 10 individual taxa) at hedge bottom and canopy level. Values for mean, median, ±SD and ±SE are shown	178
	Table 6.4. Results of Kruskal-Wallis tests (*H*) on differences between the mean full-model Akaike weightings of measures of botanical diversity as candidate explanatory variables for overall abundance of hedgerow invertebrates at ground- and canopy level and of the top 10 most abundant taxa. Post hoc Mann-Whitney *U* tests show comparisons between paired variables. Significant results are highlighted in bold. Asterisk indicates the more highly weighted variable	178
	Table 6.5a. Best models ($\Delta i \leq 2$) predicting diversity (Taxon Richness, Berger-Parker, Shannon diversity, Simpson diversity, Heip, Simpson evenness) of invertebrate taxa in hedgerows at ground level using measures of botanical diversity as explanatory variables. Explanatory variables: WTR = Woody taxon richness in the hedgerow itself; MVTRQ = Botanical taxon richness in the margin; TVTR = taxon richness of vegetation in immediate vicinity of trap	179
	Table 6.5b. Best models ($\Delta i \leq 2$) predicting diversity (Taxon Richness, Berger-Parker, Shannon diversity, Simpson diversity, Heip, Simpson evenness) of invertebrate taxa in hedgerows at canopy level using measures of botanical diversity as explanatory variables. Explanatory variables: WTR = Woody taxon richness; MVTRQ = Botanical taxon richness in the margin (quadrat); TVTR = taxon richness of vegetation in vicinity of trap	179
	Table 6.6. Comparison of the averaged full-model Akaike weightings for each measure of botanical diversity used as explanatory variables for invertebrate diversity (Taxon Richness, Berger-Parker, Shannon diversity, Simpson diversity, Heip, Simpson evenness) at both ground- and canopy level. Values for mean, median, ±SD and ±SE are shown	180
	Table 6.7. Best models ($\Delta i \leq 2$) predicting abundance of invertebrate taxa in hedgerows at ground level (upper table) and canopy level (lower table), using measures of vegetation structure as explanatory variables. Total abundance (all taxa) only shown. Variables: CQ = ground cover as measured within 2 x 1m quadrats; GL = light conditions, measured in Lux, at ground level; MSH = maximum sward height; MW = margin width	183

	Table 6.8. Comparison of the averaged Akaike weightings for each measure of ground-level vegetation structure used as explanatory variables for invertebrate abundance at both hedge bottom (upper table) and hedge canopy (lower table). Values for mean, median, ±SD and ±SE are shown	183
	Table 6.9. Results of Kruskal-Wallis tests (*H*) on differences between the Akaike weightings of the measures of ground-level vegetation structure as candidate variables explaining abundance of hedgerow invertebrates in the hedge bottom (upper table) and hedge canopy (lower table). Post hoc Mann-Whitney *U* tests show comparisons between paired variables. Significant results are in bold. Asterisk indicates the more highly weighted variable	184
	Table 6.10. Spearman rank correlations between invertebrate abundance at canopy level (all invertebrates summed and top 10 most abundant taxa) and GL (ground level light). Significant relationships are highlighted in bold and shaded. An FDR-corrected significance level of 0.017 was applied	184
	Table 6.11a. Best candidate models ($\Delta i \leq 2$) predicting diversity of invertebrate taxa in hedgerows at ground level using measures of vegetation structure as potential explanatory variables. Variables: CQ = ground cover as measured within 2 x 1m quadrats; GL = light conditions, measured in Lux, at ground level; MSH = maximum sward height; MW = margin width	186
	Table 6.11b. Best candidate models ($\Delta i \leq 2$) predicting diversity of invertebrate taxa in hedgerows at canopy level using measures of vegetation structure as potential explanatory variables. Variables: CQ = ground cover as measured within 2 x 1m quadrats; GL = light conditions, measured in Lux, at ground level; MSH = maximum sward height; MW = margin width	186
	Table 6.12. Comparison of the averaged Akaike weightings for each measure of ground-level vegetation structure used as explanatory variables for invertebrate diversity at both hedge bottom (upper table) and hedge canopy (lower table). Values for mean, median, ±SD and ±SE are shown	187
	Table 6.13. Results of Kruskal-Wallis tests (*H*) on differences between the Akaike weightings of the measures of ground-level vegetation structure as candidate variables explaining diversity of hedgerow invertebrates in the hedge bottom (upper table) and hedge canopy (lower table). Post hoc Mann-Whitney *U* tests show comparisons between paired variables. Significant results are highlighted in bold. Asterisk indicates the more highly weighted variable	187
	Table 6.14. Spearman rank correlations between invertebrate diversity at ground level and MSH (maximum sward height). All months combined. Significant relationships are highlighted. An FDR-corrected significance level of 0.02 was applied	187
	Table 6.15. Best models ($\Delta i \leq 2$) explaining the abundance of invertebrate taxa in hedgerows at ground level (upper table) and canopy level (lower table), using measures of hedge structure as explanatory variables. Explanatory variables: CL = Canopy light penetration; COA = Canopy width; HA = Height; HAA = Height of canopy above ground; HG = Height growth	191
	Table 6.16. Comparison of the averaged full model Akaike weightings for each measure of hedge structure used as explanatory variables for invertebrate abundance (total abundance and top 10 most abundant taxa) at both hedge bottom (upper table) and hedge canopy (lower table). Values for mean, median, ±SD and ±SE are shown	191
	Table 6.17. Results of Kruskal-Wallis tests (*H*) on differences between the Akaike weightings of the measures of hedge structure as candidate variables explaining abundance of hedgerow invertebrates (total abundance and top 10 most abundant taxa) in the hedge bottom (upper table) and hedge canopy (lower table). Significant results are highlighted in bold. Mann-Whitney *U* post hoc tests indicate differences between paired variables. Asterisk marks the more highly weighted variables	192
	Table 6.18. Spearman rank correlations between invertebrate abundance (all taxa summed and top ten individual taxa) at canopy level and CL (canopy light levels). All months combined. Significant results highlighted in bold and shaded. An FDR-corrected significance level of 0.017 has been applied	192

	Table 6.19a. Best models ($\Delta i \leq 2$) explaining invertebrate diversity in hedgerows at ground level using measures of hedge structure as explanatory variables: CL = Canopy light penetration; COA = Canopy width; HA = Height; HAA = Height of canopy above ground; HG = Height growth; WG = Width growth	194
	Table 6.19b. Best models ($\Delta i \leq 2$) explaining invertebrate diversity in hedgerows at canopy level using measures of hedge structure as explanatory variables: CL = Canopy light penetration; COA = Canopy width; HA = Height; HAA = Height of canopy above ground; HG = Height growth; WG = Width growth	194
	Table 6.20. Comparison of the averaged Akaike weightings for each measure of hedge structure used as explanatory variables for invertebrate diversity at both hedge bottom (upper table) and hedge canopy (lower table). Values for mean, median, ±SD and ±SE are shown	195
	Table 6.21. Results of Kruskal-Wallis tests (*H*) on differences between the Akaike weightings of the measures of hedge structure as candidate variables explaining diversity of hedgerow invertebrates in the hedge bottom (upper table) and hedge canopy (lower table). Significant results are highlighted in bold. Mann-Whitney *U* post hoc tests indicate differences between paired variables. Asterisk marks the more highly weighted variables	195
	Table 6.22. Spearman rank correlations between measures of invertebrate diversity at ground level and CL (canopy light conditions). An FDR-corrected significance level of 0.02 has been applied	195
	Table 6.23. Best models ($\Delta i \leq 2$) explaining the abundance of invertebrate taxa in hedgerows at ground level (upper table) and canopy level (lower table) using measures of landscape context as explanatory variables. Total invertebrate abundance only shown. Explanatory variables: C = connectivity (number of connections with other hedgerows); DW = distance from woodland; L = location	198
	Table 6.24. Comparison of the averaged Akaike weightings for measures of landscape context as explanatory variables for invertebrate abundance at both hedge bottom (upper table) and hedge canopy (lower table). Values for mean, median, ±SD and ±SE are shown	198
	Table 6.25. Results of Kruskal-Wallis tests (*H*) on differences between the Akaike weightings of the measures of landscape context as candidate variables explaining abundance of hedgerow invertebrates in the hedge bottom (upper table) and hedge canopy (lower table). Mann-Whitney *U* post hoc tests show significant differences only. Significant results are highlighted in bold. Asterisk indicates higher ranked variable	198
	Table 6.26. Results of Kruskal-Wallis with post hoc Mann-Whitney tests showing the difference between the ground-level invertebrate abundance at the 4 different farm locations: Nettleham (N), Potterhanworth (P), Riseholme (R), Swallow (S). Significant results are highlighted in bold	199
	Table 6.27a. Best models ($\Delta i \leq 2$) explaining invertebrate diversity in hedgerows at ground level using measures of landscape context as explanatory variables. Key to variables: C = connectivity, *i.e.* number of connections with other hedgerows; DW = distance from woodland; L = location	200
	Table 6.27b. Best models ($\Delta i \leq 2$) explaining invertebrate diversity in hedgerows at canopy level using measures of landscape context as explanatory variables. Key to variables: C = connectivity, *i.e.* number of connections with other hedgerows; DW = distance from woodland; L = location	200
	Table 6.28. Comparison of the averaged Akaike weightings for measures of landscape context as explanatory variables for invertebrate diversity at both hedge bottom (upper table) and hedge canopy (lower table). Values for mean, median, ±SD and ±SE are shown	202

	Table 6.29. Results of Kruskal-Wallis tests (*H*) on differences between the Akaike weightings of the measures of landscape context as candidate variables explaining diversity of hedgerow invertebrates in the hedge bottom (upper table) and hedge canopy (lower table). Mann-Whitney *U* post hoc tests show significant differences only. Significant results are highlighted in bold. Asterisk indicates more important variable	202
	Table 6.30. Best models ($\Delta i \leq 2$) explaining the total abundance of invertebrate taxa in hedgerows at ground level (upper table) and canopy level (lower table) using weather conditions as explanatory variables. Key to weather variables (ground level): H = humidity; R = rain; T = temperature; W = wind speed. Key to weather variables (canopy): HH = humidity handheld; TH = temperature handheld; WSH = wind speed handheld	204
	Table 6.31. Comparison of the averaged Akaike weightings for weather conditions used as explanatory variables for invertebrate abundance (total abundance and top 10 most abundant taxa) at both hedge bottom (upper table) and hedge canopy (lower table). Values for mean, median, ±SD and ±SE are shown	205
	Table 6.32. Results of Kruskal-Wallis tests on differences between the Akaike weightings of weather conditions as candidate variables explaining abundance of hedgerow invertebrates in the hedge bottom (upper table) and hedge canopy (lower table). Significant results are highlighted in bold. Mann-Whitney pairwise post hoc tests are shown for significant results only. Asterisks mark the significantly higher weighted variables	205
	Table 6.33. Spearman rank correlations showing the relationship between rainfall and invertebrate abundance in the hedge bottom (total abundance of all taxa and abundance of top 10 most abundant taxa). All months combined: April, July, September. An FDR-corrected significance level of 0.017 was applied	205
	Table 6.34. Results of Spearman rank correlations showing the relationship between Temperature and invertebrate abundance in the hedge bottom (total abundance of all taxa and abundance of top 10 most abundant taxa). All months combined: April, July, September. An FDR-corrected significance level of 0.017 was applied	206
	Table 6.35. Results of Spearman rank correlations between Wind speed and canopy-active invertebrate abundance. All months combined: April, July, September. An FDR-corrected significance level of 0.017 was applied	206
	Table 6.36a. Best models ($\Delta i \leq 2$) explaining invertebrate diversity in hedgerows at ground level using weather conditions as explanatory variables. Key to weather variables: H = humidity; R = rainfall; T = temperature; WSH = wind speed	208
	Table 6.36b. Best models ($\Delta i \leq 2$) explaining invertebrate diversity in hedgerows at canopy level using weather conditions (Silva handheld device) as explanatory variables. Key to weather variables: HH = humidity handheld; TH = temperature handheld; WSH = wind speed handheld	208
	Table 6.37. Comparison of the averaged Akaike weightings for weather conditions used as explanatory variables for invertebrate diversity at both hedge bottom and hedge canopy. Values for mean, median, ±SD and ±SE are shown	209
	Table 6.38. Results of Kruskal-Wallis tests on differences between the Akaike weightings of weather conditions as candidate variables explaining abundance and diversity of hedgerow invertebrates in the hedge bottom and hedge canopy. Mann-Whitney pairwise post hoc tests are shown for significant results only. Asterisks mark the significantly higher weighted variables	209
	Table 6.39. Results of Spearman rank correlations showing the relationship between the diversity of invertebrates in the hedge bottom and temperature. All months combined: April, July, September. An FDR-corrected significance level of 0.02 was applied	209

Chapter 1. General Introduction

1.1. The decline of biodiversity

Concerns for nature conservation and the preservation of biological diversity are relatively recent preoccupations in human society (Pullin, 2002). Historically, humans have placed themselves above nature and viewed the natural world as a resource to be exploited. This began to change in the 19th century, which saw massive increases in demands on natural resources through industrialisation and commercial expansion, but also a recognition that our ability to exploit nature to our own ends had profoundly negative consequences (Pullin, 2002). Also, in the 19th century natural historians started to ask questions about the abundance and distribution of species which led to the evolutionary theories of Darwin and Wallace. An appreciation of biological diversity began, although the term itself did not come into use until the latter part of the 20th century and appears to have been used first in 1985 for the initial planning meeting of the US National Forum on Biodiversity (Pullin, 2002). Throughout the 19th and 20th centuries, the evident loss of species fuelled a growing concern for conservation. We now find ourselves in what has been described as a global biodiversity crisis (Wilson, 1988; Faith, 2008), largely of our own making (Dirzo *et al*., 2014).

It is inexorable human population growth can be seen as the most fundamental and serious threat to the natural world (Maclean, 2010; Dirzo *et al*., 2014); the global population is predicted to reach 9 billion by 2050 (European Commission, 2012) and the UK alone is set to increase by nearly 10 million over the next 25 years (Office for National Statistics, 2015). With increasing populations comes increasing demand for living space, food and commodities, plus the attendant destruction of habitats – all key factors which lead to the decline of nature and its variety (Dirzo *et al*., 2014). Pullin (2002) speculates that we may be celebrated for putting the first man on the Moon and the information technology revolution, but are certain to be condemned for presiding over large-scale habitat destruction and the mass extinction of species on Earth. The ongoing loss of biodiversity is compromising nature's ability to support human societies (Kremen, 2005; TEEB, 2010). Rahbek (2012) asserted that the rapid loss of biodiversity was probably a greater threat than climate change. While the biodiversity crisis is arguably most acute in the tropics (Laurance, 2007), here in the comparatively less species-rich latitudes of

northwestern Europe we also have a crisis to contend with such that vital 'services' provided for us by nature are in strong decline (Dirzo *et al.*, 2014). Aside from prudential considerations with regard to our own survival, to conserve what we can, for our own future and that of generations to come, we have a fundamental ethical and moral responsibility as stewards of nature (Hooker, 1992).

1.2. The role of farming in the decline of biodiversity

As the world's most extensive industry (New, 2005a) - accounting for 38% of total land area globally (The World Bank, 2015) - it is agriculture which has had the greatest impact on our landscapes and their flora and fauna. In the millennia since Neolithic man turned from hunting and gathering to farming, the conversion of formerly wild land into farmed land, has brought destruction and fragmentation of natural habitats and wildlife populations. However, it is the increasing commitment of land to agriculture and intensification of agricultural practices in many parts of the world in more recent times that has been associated with widespread and substantial loss of biodiversity (New, 2005a). Particular species may have expanded their range in response to the expansion of agriculture, but contracted again as production methods became more intensive and semi-natural habitats were widely degraded or destroyed (Norris, 2010). The process of conversion to cropped land in particular has intensified in the 20th and 21st centuries, with a worrying trend towards less and less land resource per capita (Ramankutty *et al*., 2002). This inevitably means less space for nature.

Key practical questions are how and where do we maintain space for biodiversity, and moreover what do we conserve (Sandbrook, 2015), particularly within the constraints of the dominant land use? In order to alleviate the dominance of agriculture and the pressure placed on nature, in recent decades efforts have been made to ensure more non-crop semi-natural habitat is (re-)created side-by-side with farmland: in Europe and the UK this has been driven by changes to the Common Agricultural Policy (CAP). The CAP, launched in 1962, was geared towards productivity, to ensure the affordability of food to European consumers and living standards for farmers (European Commission, 2012). Through production-linked subsidies, it effectively encouraged the intensification responsible for habitat loss (Norris, 2010). However, reform in the last few decades has seen the emphasis shift from production to more sustainable management of precious natural resources. Farmers are seen as managers of the countryside and stewards of biodiversity. Crucially, biodiversity is acknowledged as critical for sustainable

development (European Commission, 2012). Under the reformed policy, farmers are encouraged to improve their environmental stewardship through agri-environmental payments. Environmental schemes recognize our need to take responsibility and represent an attempt to reclaim for other species some of the land given up to farming over time, by implementing conservation measures which focus on the re-creation and restoration of lost habitats. Many species have declined in range and/or numbers, but even though the human imprint on our environment is now very severe and increasing, conservation interventions can help halt, even reverse, some of the worst effects (Maclean, 2010). However, this is not a matter of fact; we have to be able to verify it and find some way to quantify it too.

1.3. The impact of farming on the diversity of the UK landscape

In the UK, intensification of agriculture in the decades following World War II has been blamed for significant declines in abundance and richness of farmland species (Robinson & Sutherland, 2002; Norris, 2010; Whittingham, 2011). On such a small island, where over 70% of the land use is agricultural (Defra, 2015), the significance of this problem seems magnified if anything.

Increasing pesticide use in the 1960s and 1970s undoubtedly contributed to the decline of farmland wildlife species, but government, the agro-chemical industry and farmers themselves were keen to demonstrate that chemical use was not the only reason for the disappearance of farmland wildlife (Hooper, 2004). As a result of concerns at governmental level, Hooper and colleagues at the Nature Conservancy's Monks Wood Centre pioneered research into connections between loss of farmland species and loss of farmland non-crop habitats, notably hedgerows (Hooper & Holdgate, 1968). As well as quantifying an alarming rate of hedgerow loss (10,000 miles a year in the 1960s), this research provided a scientific basis to recognising hedgerows as important living spaces for wildlife in the farmed environment (Pollard *et al.*, 1974; Hooper, 2004).

The group at Monks Wood were by no means the only researchers concerned for the English countryside and its flora and fauna. Cornwallis (1969), for instance, described the creation of a uniform, barren, prairie-like countryside "suited to only a limited range of 'steppe' species" created by large-scale reduction of landscape features – the removal of hedgerows was seen as a significant part of this degradation. Green (1975) lamented the changes modern intensive agricultural practices brought to the British countryside, which he described as a "diverse and beautiful *hedgerow* [my italics] landscape, rich in wildlife", but whose conversion to vast arable tracts left little room for nature conservation.

Far from being just a "gift of nature" (Dowdeswell 1987), hedgerows are of course largely a man-made feature, and have therefore historically been subject to considerations of utility by Man. Historically, their primary purpose was to delineate occupation and ownership, forming boundaries between parishes and fields and stock-proof barriers. Hedges and other boundary features in hillier parts of the country often date back to Celtic or Norse times (Tinker 1974). However, the network of hedgerows characterising lowland Britain, and arable farmland (*e.g.* in Lincolnshire), owes more to the 'enclosures' of 1700 to 1850, when open fields and common grazing were fenced off ("enclosed") into smaller fields (Tinker, 1974).

Advances in agriculture, the need for higher productivity and the rise of arable farming brought increased mechanisation and industrialisation of the agricultural landscape during the latter part of the 19th and into the 20th centuries. Arable farming necessitated larger fields: farm machinery could only be efficiently deployed in fields of sufficient size. Hedgerows lost their original utility, became an inconvenience to landowners, and as a consequence were indiscriminately grubbed up (Dowdeswell, 1987).

Apart from enabling access to fields by large farm machinery, other practical reasons for removing hedgerows included: easier maintenance of ditches; the need to control rabbits; to prevent weeds from spreading into fields; to eradicate a reservoir of potentially harmful invertebrate pests; to reduce maintenance costs; and to gain extra land (Tinker, 1974). Hedgerow removal, for any one or a variety of these reasons, has been going on for over 200 years (Dowdeswell, 1987), although the pace of removal increased dramatically in the 20th century. Dowdeswell (1987) estimated that during the period of maximum farming intensification between 1946 and 1974 approximately 230,000 km of hedges disappeared in the UK; losses were particularly heavy in flat open arable areas such as the East of England.

Parliamentary debates reveal that grants were available to farmers specifically for the *removal* of hedgerows until 1976 (Hansard, 1987), and when protection for hedgerows was debated by parliament during the mid-1990s in the context of the Environment Bill, concerns were raised over the continued grubbing out of farmland hedges (Hansard, 1995a; 1995b). Substantial removal of hedgerows and other non-crop habitats meant that agricultural landscapes have changed from landscapes characterised by numerous small, extensively managed farms with a diverse range of land uses, to landscapes dominated by a much smaller number of intensively managed, specialised farms. They have become more

homogenous and less diverse as a result (Benton *et al*., 2003). It was not until the mid-1980s, and the advent of agri-environment schemes (AES) in the UK, that government funds started to pay farmers for restoring wildlife habitats (Grice *et al*., 2007).

Despite large-scale decline, hedgerows nonetheless remain the most widespread semi-natural habitat in England, Wales and Northern Ireland. The national stock of 'managed' hedges for England is reckoned to be circa 400,000 km, reduced from 450,000 km in 1998 (Natural England, 2009). In fact, over large parts of the lowlands, including Lincolnshire where this project was based, they are the main surviving semi-natural habitat. Such living space has to be important in a part of the UK which counts amongst the most intensively cropped areas in the world (Ramankutty *et al.*, 2002).

1.4. The value of farmland hedgerows as wildlife habitat

As we have seen, historically hedgerows were not created explicitly for the purpose of enhancing wildlife. Only in the latter part of the 20th century, because of heightened environmental awareness and a concern for the impacts of farming on biodiversity, has their role as 'reserves' for a diversity of wildlife species became more explicit. Nonetheless, despite several decades of investment in conserving and enhancing hedgerows they remain under threat and in decline, with losses attributed to a combination of poor management and insufficient new planting (Bealey *et al*., 2009; Wolton, 2011; Staley *et al*., 2012a). It is therefore important to revisit and re-examine their contribution to our countryside, not only to the beauty of our landscape, but to a host of wildlife. A canon of literature on hedgerows from the last 50 years already exists, yet their current state and value to nature, particularly in agro-ecosystems, clearly warrant further investigation (Staley *et al.*, 2012a).

Hedges even have their own dedicated agency, a partnership of governmental and charitable organisations, Hedgelink. Hedges have merited conferences in their own right, notably the Institute of Landscape Ecology's 2001 meeting on world hedgerows and most recently "Hedgerow Futures" (Dover, 2012), exploring the fate of the hedgerow in the UK and Western Europe. This is a clear indication of the importance of hedgerows, be that in our hearts and minds or a demonstrable ecological fact.

Because of their importance as a component of our landscape, hedgerows form a prominent component of efforts to maintain biodiversity in the agricultural environment (Natural England, 2009). However, there is evidence that we are still losing them faster than we can replace or restore them (Natural England, 2009), without really knowing what

the implications are for biodiversity (Faith, 2008). Even in supposedly familiar landscapes, close to home, we may have unknown variety with unknown value.

Hedgerows are deemed to be of critical importance to the existence of numerous plants and animals, in particular many groups of invertebrates (Holland & Fahrig, 2001; Hedgelink, 2009; Butterfly Conservation, 2014). Despite the value of hedges as nature reserves and wildlife corridors being widely acknowledged, from the earlier investigations at Monks Wood to more recent times (*e.g.* Hinsley & Bellamy, 2000; Bennett, 2003; Bealey *et al.*, 2009; Hedgelink, 2009; Defra, 2011a; RSPB, 2012; PTES, no date), there are also indications that the benefits are not universal for all species (*e.g.* Gruttke, 1994; Burel, 1998; Davies & Pullin, 2007). For instance, a 'barrier' effect, preventing free dispersal of wildlife, has been noted by some (*e.g.* Dover & Sparks, 2000). Also, a detrimental fragmentation effect on habitat continuity has been implicated in bird population declines, where hedgerows effectively split up grassland into 'parcels' too small to adequately support passerine abundance or diversity (Besnard & Secondi, 2014). Others suggest that farmers are focusing too much on hedgerow and margin management instead of modifying the management of the productive parts of fields, to the detriment of farm species, such as ground-nesting birds which are dependent on nest and feeding resources being available in-field rather than in the hedges and margins (Butler *et al*. 2007). Nonetheless, Usher (1997) believed that at worst hedgerows may be neutral in the maintenance of biodiversity in agricultural landscapes, and at best vital. Maclean (1992) describes a hedge as being "a thin strip of woodland" and the adjacent field margin "a strip of meadow". Both analogies draw attention to the perhaps idealistic ambitions for the restricted area between crops.

1.5. The benefits of farmland hedgerows to invertebrate diversity

Invertebrates as a whole are even more important in the maintenance of ecosystems than vertebrates (Wilson, 1987). They make up a substantial component of the diversity of life on Earth – anywhere in excess of 50% (Wilson, 1994) to over 75% (Pullin, 2005, citing Groombridge, 1992) of the 1.2[1] million or so described species on Earth (Mora *et al.*, 2011). They are the multitude of "little things that run the world" by underlying many essential processes without which ecosystems could not function (Wilson, 1987). Yet Dirzo *et al.* (2014) acknowledge that the loss of invertebrate biodiversity globally has attracted much less attention than that of vertebrates, despite the crucial roles they fulfill.

[1] Wilson (1994) indicates 1.4 million species and Pullin (2005) 1.5 million.

In Great Britain there are over 30,000 species of non-marine invertebrates (Matt Shardlow, personal communication) and 24,000 species of insects (Barnard, 2011), accounting for approximately 40% of the total fauna of this country.

Invertebrates are fundamental components, numerically and ecologically, of agricultural ecosystems, encompassing a vast range of more or less beneficial species; pests, predators, pollinators, parasitoids, scavengers and detritivores (Alford, 1999; New, 2005a)**.** In an analysis of four major groups (Coleoptera, Hymenoptera, Lepidoptera and Odonata), Dirzo *et al.* (2014) showed that in the UK 30 – 60% of species per Order have suffered declining ranges over the past 40 years. Invertebrates also form a significant food resource for many other farmland species and so their loss has consequences for other fauna: a general decline in insect abundance on intensively-cultivated farmland has, for instance, been implicated in farmland bird decline (Benton *et al.*, 2002).

Declines in invertebrate numbers and diversity have been connected in particular with loss of habitat, such as hedgerows, which provide foraging and shelter for a host of species. Within farmed landscapes, hedgerows can provide an important non-crop habitat or 'reservoir' for a wide variety of plants and animals, of which invertebrates constitute the vast majority of species (Pollard *et al.*, 1974; Dowdeswell, 1987; Maudsley, 2000; Wolton & Vergette, 2012). In the case of invertebrates, experts are in no doubt that habitat destruction and fragmentation of the type caused by removal of landscape features or decline through poor management, such as woodland and hedgerows, has been and remains probably *the* major threat to diversity in agro-ecosystems (*e.g.* New, 2005; Goulson, 2010; Stubbs, 2010; Thomas, 2010), ahead of other significant drivers of change in wildlife such as pesticides, invasive species and, increasingly, climate change (Maclean, 2010).

The status of hedges as important non-crop habitats for a diversity of invertebrates has been emphasized by a succession of researchers, ranging from those investigating single hedges (Lewis, 1969a, 1969b; Wolton & Vergette, 2012), to others studying a wider variety of hedges (Pywell *et al*., 2005; Pollard & Holland, 2006; Deeming *et al*., 2010; Bennett *et al*., 2013) Pollard & Holland (2006) recorded the abundance and diversity of arthropods in a selection of farmland hedgerows. More than 600 plant species, 1,500 insects, 65 birds and 20 mammal species have been recorded in hedgerows (Reid & Grice, 2001). A more recent on-going assessment of hedgerow biodiversity (albeit based on a single organic farm hedgerow in Devonshire) indicates the presence of circa 1,700 species

of plant and animal, of which approximately 1,400 are insect species with many hundreds of parasitic Hymenoptera left to identify (Wolton & Vergette, 2012). The extent to which this could be representative of other hedgerows in other parts of England under different farming systems is uncertain.

The wildlife value of farmland habitats including hedgerows has typically been evaluated by studying the most apparent and charismatic taxa as 'indicators' or 'surrogates' of wider biodiversity, often birds (*e.g.* Hinsley & Bellamy, 2000) and small mammals (*e.g.* Bates & Harris, 2009). Certain invertebrates, albeit often the most detectable or economically important groups, notably butterflies, bees and beetles, pest herbivores and their predators have also been well-studied (*e.g.* Maudsley, 2000; Maudsley *et al.,* 2002; Griffiths *et al.*, 2007; Flohre *et al.*, 2011; Defra, 2011). There is however debate on the value of selectively using surrogates to indicate overall faunal diversity and suggestions that the study of communities and assemblages, as a 'coarse filter' or 'higher taxon' approach, has its merits in addressing the problem of assessing general invertebrate diversity (Gaston and Williams, 1993; Duelli *et al*, 1999; Samways, 2005). New (2005) also concedes that due to the impracticality and expense of identifying thousands of invertebrates down to species, identifications down to Family or Order level may be "an important, financial expedient shortcut in invertebrate biodiversity surveys", provided they are of consistent quality and accuracy. Biaggini *et al*. (2007) found that assessment of invertebrate diversity to Order level is capable of discriminating between different land uses and could have a use at least in initial rapid biodiversity assessment in agricultural landscapes at local scale. Holland & Fahrig (2001) also recommended field studies on broad taxonomic groups. Further investigations relating to conservation value of hedges are still needed to establish the dependency of the vast range of invertebrates on hedgerows, including less well-documented taxa (Maudsley, 2000; Barr *et al.*, 2005; Staley *et al.*, 2012).

1.6. Agri-environmental protection of hedgerows

Alongside protection of hedgerows in legislature is protection through policy, and practical application of that policy through environmental management measures. The European Union's Common Agricultural Policy (CAP) is the key instrument for delivering environmental protection and improvement in the farmed environment, through which farmers are paid for managing natural resources sustainably. Under this policy, farmland hedgerows in the UK are first and foremost protected under so-called 'Cross

compliance', overseen by the Rural Payments Agency (RPA), which is a fundamental requirement for farmers to comply with a set of Statutory Management Requirements and keep their land in Good Agricultural and Environmental Condition (GAEC) in order to qualify for subsidies (RPA, 2013). There are two GAEC standards relating to the protection of hedgerows, acknowledging that a hedgerow comprises both a grassy verge and a woody component: GAEC14, relates to the minimum 2m protection zone either side of hedgerows and along ditches (RPA, 2013), and GAEC15, relates to the management of hedgerows themselves. Inspection statistics, while they show a low level of failure under GAEC15, indicate an increasing breach of GAEC14 conditions in the last few years, to do with both ploughing and pesticide application within the protection zone (RPA, 2013). Reforms of farming policy have led to new GAEC category definitions from 2015, which place hedgerows into a collective 'boundaries' group. It is unclear what this means for protection or inspection of hedgerows, although extension of the no-trimming period to run from March to the end of August seems a positive step (Defra, 2014).

In addition to the statutory requirements of Cross Compliance, the importance of hedgerows in the farmed landscape is also recognized through special voluntary measures, *i.e.* options to create/restore and manage them under (AES). In fact, hedgerow options are amongst the range of Priority Options under Entry Level Stewardship (ELS), the more widespread basic scheme (Hodge & Reader, 2010; Natural England, 2012a), and under Higher Level Stewardship (HLS), which has more focused conservation goals (Natural England, 2012b; 2013). The success of AES options, unlike basic Cross Compliance requirements, tends to be measured in terms of uptake (Ledder, no date)[2]. Hedgerow management options were the Top 2 options under ELS, included in >50% of agreements, while hedgerow planting and restoration options were among the top 20 options for HLS, included in 19% and 39% of agreements respectively. Approximately 164,000 km of hedgerow are under AES and in excess of 21,000 km of hedgerow have been restored/created (Natural England, 2009). There remains some concern over whether steps taken to halt the decline of hedgerows have been sufficient, with calls for further new planting as well as restoration efforts (*e.g.* Wolton, 2011). Further 'losses'[3] of hedgerow

[2] Defra's Analysis and Evidence Team which is responsible for annual Farm Surveys do not maintain up-to-date data on the uptake of environmental stewardship options (Lisa Richardson, personal communication, Nov 2013)

[3] Whether an unmanaged relict hedgerow would be considered a loss to wildlife is a different question.

stock are attributed to lack of management which has seen an increase of relict hedgerows to 145,000km (Hedgelink, no date d).

1.7. Measuring the achievements of AES and hedgerow conservation

The high level of uptake of hedgerow options is not necessarily matched by investment in studies dealing with hedgerow biodiversity and farming interactions. Different interest groups, research agencies such as the Centre for Ecology and Hydrology, charities, policy makers, academic institutions and the National Farmers Union - produce their own assessments (Boatman *et al.* 2007; 2010a; 2013; Dover, 2012), but this does not amount to consistent or coordinated monitoring of outcomes. To give a little further context, Randall & James (2012) made a systematic analysis of evidence for European farmland conservation success covering an extended period from 1960s to 2010. Regarding the impact of agri-environmental options, they identified 11 studies on hedgerows for 'temperate' (*i.e.* north-western and eastern) EU countries overall.

Hedgerow planting as habitat creation should presumably serve to improve agri-environmental conditions and promote biodiversity, but its effectiveness requires monitoring. Investigators have regularly questioned the benefits of AES options such as hedgerow planting and management, because, despite over 25 years of science, policy and financial inputs, there is mixed evidence for beneficial effects (Whittingham, 2007, 2011; Boatman *et al.*, 2010a, 2010b; Kleijn *et al.*, 2011), with some studies reporting wildlife benefits (*e.g.* Hof *et al.*, 2010) and others suggesting that farmland hedgerows may not be delivering the anticipated returns (*e.g.* Bates & Harris, 2009). Herzog (2005) described AES as a "landscape experiment", whereby outcomes may be somewhat uncertain, as is the nature of experimentation.

To an extent, research has been able to quantify the role of farming intensification in the decline of biodiversity (*e.g.* Stoate *et al.*, 2001; Benton *et al.*, 2002; Benton *et al.*, 2003; Butler *et al.*, 2007; Staley *et al.*, 2013). Robinson and Sutherland (2002) noted that generally amongst farmland species declines have been particularly marked amongst habitat specialists; many of the taxa still common on farmland are habitat generalists. This fits with the observed 'homogenisation' of the farmed landscape (Benton *et al.*, 2003).

Numerous farmland species, notably birds and butterflies continue to decline, some at a rapid rate (Natural England, 2009). Defra/JNCC's (2013) data on the main farmland animal biodiversity indicators, demonstrate that the declines amongst farmland birds and butterflies continue. In the UK 'specialist' farmland bird populations have declined by

73% since 1970, whereas generalists are less affected at just 2% below 1970 (BTO/RSPB, 2014). Indices for specialist passerine invertebrate-eaters in England shows these species are down in number with, for instance, long-term declines of 80% for the Starling (*Sturnus vulgaris*) (Defra/JNCC, 2014). An experimental pollinating insects index was added to the Government's biodiversity indicators in 2014 and shows that 70% of bee species declined between 1980 and 2010 (Defra/JNCC, 2014). Butterflies bounced back after a wet summer in 2012, but the long-term trend is still general decline (Fox *et al.*, 2011; Davies, 2014). Lack of shorter-term progress (2007-2012) for farmland species – *e.g.* farmland bird specialists and generalists experienced significant declines during this period of 9% and 5% respectively - is also of concern as this has occurred despite statutory protection of species and of habitats and in spite of investments in farming for wildlife through agri-environmental schemes (AES).

Some reviews of research have established only weak associations between AES and a positive contribution to increased biodiversity (Kleijn and Sutherland, 2003; Kleijn *et al.*, 2006; Whittingham, 2011). Furthermore, making an assessment of AES for biodiversity other than birds is severely hampered by rather vague scheme objectives for other groups, a poorer understanding of the links between land-use change and populations, and rather patchy data (Norris, 2010). Further studies, with more quantitative data, are evidently needed in order for the benefits of AES, particularly for invertebrate biodiversity, to be better evaluated. Although evaluations of what has been achieved for other taxa by AES, particularly farmland birds, seem not to be in short supply (Boatman *et al.*, 2010), commentators admit that despite "good evidence" that AES has been delivering "significant biodiversity benefits", there is less evidence for mammals and invertebrates than for plants and birds (Boatman *et al.*, 2008). How current agricultural practices affect the conservation value of non-agricultural habitats, such as hedgerows, how detrimental impacts can be mitigated, plus lessons learned from AES with regard to its role in optimizing biodiversity are among the top 10 policy-relevant ecological questions for farming in the UK identified by Sutherland *et al.* (2006).

1.8. Evidence for the benefits of AES hedgerow options to invertebrate diversity

Our understanding of what is happening in the farmed environment, and of the impacts of AES, is to an extent inhibited by a partial and fragmented view, because of the way the literature has been dominated by single taxon studies (*e.g.* Carabid beetles). This is due in part to the impracticality of concentrating conservation efforts at species level for

the whole spectrum of such large taxa as invertebrates. There is consequently a relative paucity of studies attempting to evaluate broad spectrum invertebrate diversity of hedgerows, despite an acknowledged need for them (Staley *et al*., 2012a). Pollard & Holland's (2006) study of hedgerow canopy invertebrates is a notable exception, examining the full range of invertebrate taxa at ordinal and family level. Commentators have called for further investigation of the importance of hedgerows to invertebrate biodiversity and the potential for improvement through management of farmland hedgerows (*e.g.* Holland & Fahrig, 2001; Marshall *et al.*, 2001; Britt *et al.*, 2005; Bealey *et al.*, 2009). There is also an acknowledged need by Natural England for evaluating whether AES measures have been and are being effective at protecting invertebrate biodiversity at both the landscape and local scale (Boatman *et al*., 2008; Dr Geoff Radley, personal communication, October 2012[4]).

Recent work on hedgerows at the Centre for Ecology and Hydrology indicates that there are still questions to be asked regarding conditions for invertebrates in AES hedgerows (Staley *et al.*, 2012; 2013; Amy *et al*., 2015) and that there is by necessity a revisiting of what can be achieved in terms of invertebrate conservation by bolstering hedgerow habitats. Hedgerow management and planting have formed such popular options under AES that they demand further investigation. They are of continued importance and there is an obvious need to monitor what has been achieved (Boatman *et al.*, 2007; 2010; 2013). AES monies are now focused on improving management, but there are also calls for more planting to be done (Wolton, 2011) to replace hedgerow stock that is now being lost to poor management rather than direct removal. The effectiveness of such measures requires monitoring. Given the considerable investment in planting and maintenance of hedgerows under AES, what have been the benefits?

1.9. Hedgerow planting – beneficial effects on invertebrate populations?

Assessing the benefits of AES for biodiversity other than birds is "severely hampered by rather vague scheme objectives for other groups and a poorer understanding of the links between land-use change and populations" (Maclean, 2010). The study described in this thesis is a contribution towards filling the apparent deficit of evidence for delivery of biodiversity benefits under AES, by investigating what hedgerow planting has

[4] Dr Geoff Radley (Natural England) - member of LUPG which was a union of the UK's conservation agencies. The LUPG sought "to develop a UK-level understanding of the environmental and delivery implications of policy scenarios related to land use, particularly farming and forestry".

contributed towards biodiversity and more particularly towards invertebrate biodiversity. In this respect, it ties in with two of the key questions in ecology: how we measure progress towards a wider sharing of resource between humans and wildlife and how we might effectively monitor invertebrates, especially where they are resources for other taxa (Maclean, 2010). Specifically, it explores the nature of invertebrate assemblages in newly-planted hedgerows, how this can be measured, whether it demonstrates beneficial effects and the extent of those effects.

My previous work at undergraduate level investigated the effect of age/maturity on hedgerow invertebrates and concluded that older hedges were associated with greater diversity in the invertebrate assemblage at ground level in the hedge bottom, but that new hedges relatively quickly acquired the characteristics of their mature counterparts (Deeming *et al.*, 2010). These conclusions were, however, based on a small number of hedges at a single farm site and the investigations described here are a considerable expansion of that study, encompassing also the woody part of the hedge itself. Invertebrate assemblages of both the ground environment and the hedge canopy were investigated using a greater sample size spread over a wider geographical area.

The project addressed the question of how hedgerows, newly-planted under AES in the last decade or so, might contribute to or complement an existing stock of 'mature' hedges (dating back >50 years), and indeed whether, hedgerow age, may impact invertebrate biodiversity and the role of other structural and botanical factors which may be associated with the history of the hedgerows. The question of how we measure any benefits to biodiversity was also addressed: rather than looking at one or two species or groups, the study takes a broad spectrum approach, suited to rapid assessment (Biaggini *et al*., 2007) of invertebrate fauna, including those taxa considered to be under-represented in hedgerow studies. Locations include the University of Lincoln's own arable farmland sites and two other farms in Lincolnshire, which presented an opportunity to explore this theme, as hedgerows had been restored/created under AES as part of Stewardship agreements.

In particular, the invertebrate fauna of hedges, assigned as either 'Mature' or 'New', were surveyed. Inverted commas are used to indicate that these terms used to describe age categories are comparative. By comparing the abundance and diversity of invertebrates in the mature hedgerows, with that of hedgerows recently planted under AES, the objective was to assess whether maturity (or age) of a hedgerow habitat can have a significant effect on the diversity of invertebrate populations and also by implication of the

effectiveness of government-subsidised hedgerow-planting as a means to sustain and enhance biodiversity.

It was predicted that: 1) The hedges would differ significantly in their invertebrate fauna, both in terms of abundance and diversity, due to their different maturities; 2) Invertebrate fauna of the hedge bottom and hedge top in Mature hedges would be taxonomically richer and more diverse than hedgerows consisting of new planting under AES. This latter hypothesis relates to a stability-diversity principle, which states that the longer a community/assemblage exists and the longer ecological conditions have persisted, the more diverse an ecosystem is (Thienemann, 1956; McIntosh, 1985).

Interactions between hedgerows, their invertebrate faunas and other influential factors besides habitat maturity, such as time of year, hedgerow structure, botanical diversity, weather were investigated. The effectiveness of invertebrate trapping methods and measurement of diversity were also evaluated.

The characteristics of invertebrate diversity in my 'New' and 'Mature' farmland hedgerows are investigated in subsequent chapters. Chapter 2 discusses the key topics for measurement and analysis in hedgerow research. Chapter 3 describes the methods for the sampling and measurement of invertebrate biodiversity and its determinants. Chapter 4 explores the application of a sticky trapping technique for sampling invertebrates at ground-level, the possibilities for bio-indication and the measurement of invertebrate diversity in the hedge bottom. Chapter 5 explores the application of a beating technique for sampling invertebrates at hedge canopy-level, again with the possibilities for bioindication and the measurement of diversity in the hedge top. In Chapter 6 a selection of biotic (notably botanical diversity and structural features) and abiotic factors (weather) as discussed are modelled to explore their strength as determinants of invertebrate diversity in hedgerows. Finally, Chapter 7 discusses findings from my investigations in these key areas, in the context of continuing developments in AES, the conservation of farmland hedgerows and invertebrate diversity.

Chapter 2. Literature review

2.1. Introduction

The importance of hedgerows to a diversity of wildlife has long been emphasized, culminating in various protections, notably the Hedgerow Regulations 1997, inclusion amongst Biodiversity Indicators (in conjunction with woodland) (Defra 2013a), and UK BAP priority habitat status. Hedgerows remain a habitat of principal importance in England under the "UK Post-2010 Biodiversity Framework" (JNCC, no date). Their widespread nature and perceived importance in the farmed countryside is reflected in the popularity of agri-environment scheme (AES) options for hedgerow planting, management and restoration in AES (Hedgelink, 2014).

The importance of hedgerows and their role in supporting a diversity of invertebrates is also reflected in a body of work over time from Hooper & Holdgate (1968) to the near present (Staley *et al*., 2012a). Investigations have, however, been perhaps surprisingly few given their extent as a wildlife habitat in the farmed landscape and the repeated emphasis on how important they are to that wildlife. A citations search on Web of Science™ (Fig. 2.1.), which is indicative rather than exhaustive, points to a sustained but relatively low level of activity, also reflected in findings by Randall & James (2012). The latter called for further evidence for the efficacy of AES measures, including hedgerow options. Given the monetary investment in hedgerows under AES, this habitat warrants further scrutiny in terms of what it is capable of delivering.

In this review, I summarise some of the key findings of previous work on farmland hedgerow ecology in the UK/England. More specifically, the summary reviews literature concerning the value of farmland hedgerows to invertebrate biodiversity and the factors influencing invertebrate populations. It also examines the use of invertebrate sampling techniques for use at both the hedge bottom and hedge canopy and discusses the relative merits of methods to assess invertebrate diversity using indicators and indices.

2.2. Farmland hedgerows as invertebrate habitats – research themes over time

2.2.1. Increasing emphasis on invertebrate diversity

Interest in the ecology of farmland hedgerows in Britain can be dated back to the 1960s when investigations began into the consequences of hedge removal for wildlife (Hooper & Holdgate, 1968; Lewis, 1969a; 1969b). The seminal monograph on hedgerows,

their history, flora, fauna and role in a farmed landscape appeared in 1974 under the New Naturalist title "Hedges" (Pollard *et al.*, 1974) derives from these investigations. In the subsequent 40 years, further books, studies, research papers and even entire conferences have followed, dedicated to aspects of the natural history and ecology of hedgerows (*e.g.* Rackham, 1976; Rackham, 1986; Dowdeswell, 1987; Lee, 1985; Muir & Muir, 1987; Watt & Buckley, 1994; Barr *et al.*, 1995; McCollin, 2000; Barr & Petit, 2001; Barnes & Williamson, 2006; Dover, 2012).

The emphasis of investigations has shifted over time, since the 'inception' of hedgerow research in the 1960s. Whereas the focus once used to be on surveying and documenting the natural history of hedgerows, the approach appears increasingly 'utilitarian' and investigators focus on farmland hedgerows (and other non-crop habitats) what they can 'deliver' in terms of ecosystem services, such as pollination and biological control. For example, Macfadyen *et al.* (2011) have shown that hedgerows are capable of making a useful contribution to maintaining a diversity of parasitoid insect species likely to provide agricultural pest control services. This reflects the largely utilitarian concerns of conventional agricultural and our reliance on invertebrates, and their diversity, to support our needs. A bibliographic search of Thomson Reuters™ Web of Science™ from the past 30 years, the period in which the term 'biodiversity' has been in use, shows comparatively little investigation of hedgerow invertebrate diversity *per se* (Fig. 2.2).

There are evident deficits in our knowledge of the diversity of hedgerow invertebrates in the UK. For instance, Maudsley (2000) lamented a "paucity" of data on invertebrates (other than butterflies), which he attributed at least in part to the difficulty in obtaining representative samples of the inherently variable faunal composition of hedgerows. Maudsley (2000) also highlighted the awkwardness and impracticality of sampling invertebrates from often dense woody structures as a potential barrier to investigations. However, he also observed that such challenges should act as an incentive for investigations not a deterrent.

Barr *et al.* (2005) provided an extensive review of hedgerow literature, but the section on invertebrates serves to highlight that the majority of studies up to that time had been devoted to understanding the use of hedgerows by beetles (notably Carabids) and butterflies. Studies had tended to focus on species diversity within single taxa and/or functional groups (*e.g.* predatory arthropods such as spiders, pollinators such as

bumblebees, and Hemipteran pests). Barr *et al.* (2005) also reviewed the historic and ecological roles of hedgerows in supporting invertebrate biodiversity in agricultural environments (as corridors, networks, barriers). The success of different hedgerow management techniques were explored, although not explicitly in the context of AES in order to measure the outcomes of Environmental Stewardship.

Boatman *et al.* (2008) assessed AES and their delivery of benefits to biodiversity, including hedgerow options and observed that there was 'good evidence' that UK AES had delivered *significant* benefits to biodiversity for the plants and birdlife of hedgerows. They

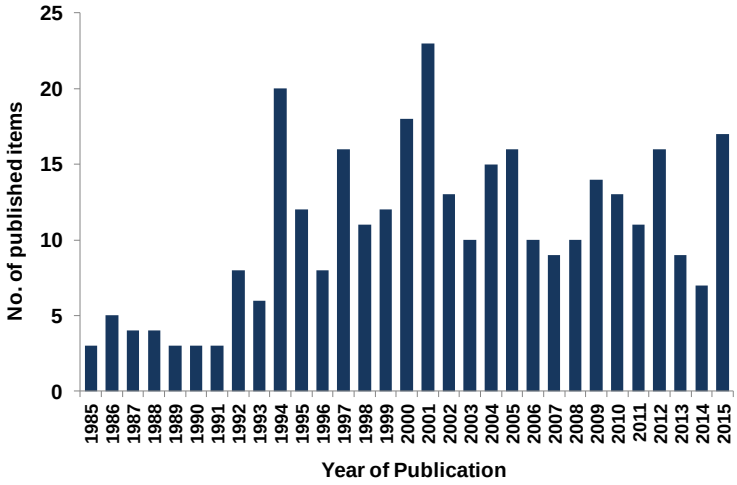


Figure 2.1. Annual number of published items 1985 - 2015 for the search terms "hedgerow*" AND (UK OR United Kingdom OR GB OR Great Britain OR England) as topics. Source: Thomson Reuters™ Web of Science™. Correct 01 February 2016

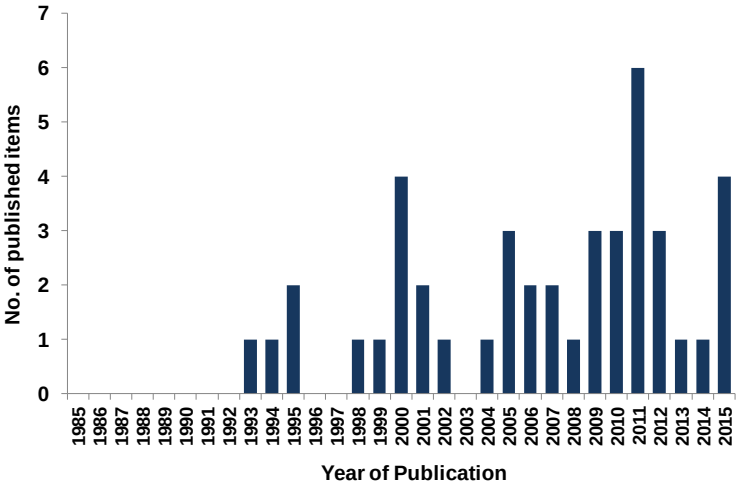


Figure 2.2. Annual number of published items 1985 – 2015 for the search terms "hedgerow*" AND (invertebrate* OR insect* OR arthropod*) AND (diversity OR biodiversity) AND (UK OR GB OR Great Britain OR United Kingdom OR England) as topics. Source: Thomson Reuters™ Web of Science™. Correct 01 February 2016

also stated that, there was less evidence for beneficial effects of AES for other taxa, notably mammals and invertebrates, especially in arable habitats and the existing evidence consisted of cases of single taxa, such as bumblebees, sawflies and plant bugs.

Invertebrates are a frequently studied group in agro-ecosystems, they also constitute the vast majority of species within hedgerows, yet there is comparatively little published research on the invertebrate communities/assemblages of hedgerows, as opposed to individual taxa (Marshall *et al*., 2001). Pollard & Holland (2006) and Amy *et al*. (2015) are notable exceptions from the last decade. Research on the benefits of agri-environmental measures has however tended to focus selectively on individual arthropod taxa, particularly more 'charismatic' or distinctive groups, such as beetles (notably Carabids and Staphylinids), bees, butterflies, moths and spiders (*e.g.* Sotherton 1984; Barr *et al*., 1995, 2005; Thomas and Marshall, 1999; Burel *et al*., 2004; Pywell *et al*. 2005; Field *et al*. 2007; Griffiths *et al.*, 2007; Flohre *et al*., 2011; Fischer *et al.*, 2013; Facey *et al*., 2014; Hanley & Wilkins, 2015). These are often used as 'proxies'/'surrogates' or general bio-indicators of habitat quality for farmland invertebrates as a whole.

Aside from predatory arthropods such as Carabid beetles, we probably know most about the herbivorous inhabitants of hedgerow habitats, thanks to extensive knowledge of plant and insect associations recorded in the Biological Record Centre's Database of Insects and their Food Plants (DBIF). Staley *et al.* (2012a) echoed Barr *et al.* (2005) in suggesting that a functional view of hedgerow invertebrate diversity, with a concentration on herbivorous pests, predators, and pollinators has probably prevented a true appreciation of the biodiversity of farmland hedgerow fauna. They re-emphasized a need for more inclusive investigations of hedgerow invertebrates, to embrace more cryptic, less charismatic hedgerow organisms, including truly hedge-dependent organisms, *e.g* Psocoptera. Results shown in Fig. 1.2 suggest that research has not moved much in the desired direction in the past decade, although work by the Centre for Ecology and Hydrology has yielded insights into the effects of management techniques on functional diversity (*e.g.* Amy *et al.*, 2015). Studies of the invertebrate fauna of single hedges, such as that undertaken by Wolton & Vergette (2012) on organic farmland, are valuable, but are unlikely to reflect conditions on the dominant land use of conventionally farmed arable, even where Environmental Stewardship is in place. Kromp (1999), for instance, found that organic farms 'almost always' had greater (Carabid) species richness than more intensively-farmed land.

2.2.2. Hedgerow age and invertebrate diversity

A relatively small number of studies have examined the role of hedgerow 'maturity' in supporting invertebrate populations, with mixed responses shown for a limited number of individual taxa. Pollard *et al.* (1974) reported experimental work at Monk's Wood which indicated that 10-year-old hedges had a relatively good colonisation rate by a range of the more common butterflies, by comparison with bird species. Cameron *et al.* (1980) showed that snail diversity increased with age of hedge but that the effect was slight in hedges above 100 years old. By contrast, Gruttke & Kornacker (1995) concluded that 9-year-old hedge plots (part of mitigation for a road infrastructure project) were of limited value as habitats for a selection of largely ground-active invertebrate species, especially Carabid beetles. Lechner (1991) found that 5-year-old field hedgerows had more species of beetle and arachnid than neighbouring mature habitats and Bergthaler (1996) concluded that even newly-planted hedgerows are important successional landscape features capable of harbouring a diversity of spider and harvestman species. In one Austrian study, a 3-year-old hedge had more ground beetles than 5-, 9- or 40-year-old hedges (Kromp & Hartl, 1991, unpublished). By contrast, Clements & Alexander (2004) showed positive correlations between saproxylic invertebrate diversity and hedgerow age, concluding that old hedgerows are an important habitat for this group. Pywell *et al.* (2005) found some evidence for an effect of hedge age, albeit on a limited range of species of over-wintering beetles and spiders at ground level. For abundance and diversity in general there was no difference between the younger (2-5 years old) and more mature (40-60 years old) habitats. Deeming *et al.* (2010) investigated the invertebrate assemblage of all taxa captured in the bases of a small number of hedgerows of differing ages under Stewardship on Lincolnshire farmland. They found mature hedgerows (>50 yrs) had greater invertebrate diversity than newly planted hedgerows (≤5 yrs).

Further evaluations of associations between broader spectrum diversity and the heterogeneity of structural and botanical composition of hedgerows, as determined by growth form and age, are considered desirable (Dennis *et al.*, 1994; Maudsley, 2000; Benton *et al.*, 2003). Britt *et al.* (2005) concluded that there was an urgent need for up-to-date surveys of the invertebrate populations of hedgerows, and for more comparative data on different hedge types.

2.2.3. The dating of farmland hedgerows

In an extension of investigations by Deeming *et al*. (2010), my study compared the invertebrate abundance and diversity of hedgerows of different ages, notably those newly-planted under AES and more mature habitats. Accurate determination of the age of mature hedges is, however, difficult. The plant composition of the hedgerow can also be a clue to ageing a mature hedgerow where records are lacking. Historically, hawthorn (*Cretaegus* spp.) has been a favoured species for hedgerows in the British Isles, because it provided a stock-proof barrier – not for its aesthetic appeal or ecological value (Dowdeswell, 1987). While there is evidence that the presence of a high proportion of Midland hawthorn (*Cretaegus laevigata*) indicates ancient origins for a hedge, the presence of higher quantities of Common hawthorn (*Cretaegus monogyna*) is associated with the late Enclosure period during the 19th century and thereafter (Dowdeswell, 1987).

Hooper's hypothesis is another means of estimating the age of a hedgerow (Barnes & Williamson, 2006). Although still used as a valid means of hedge dating (*e.g.* in the Hedgerow Survey Handbook, 2007), the hypothesis (as a rule of thumb 100 years per woody/shrubby species found in a 30 yard length of hedge) is subject to large variations (Pollard *et al*., 1974), and could vary by as much as 200 years either way (Hooper, 2004). The age/number of species relationship in Hooper's Hypothesis does not necessarily hold true, as it assumes a consistent rate of colonisation. And while research does suggest that, in general terms, botanical diversity will increase with age, old hedgerows can also decline in species richness over time (Garbutt & Sparks, 1999). In fact, Barnes & Williamson (2006), reviewing the efficacy of hedgerow dating techniques, concluded that topography, soil type and moisture may be a more important determinant of botanical species content than age *per se*.

Muir (2000) emphasizes the importance of examining historical records and 'reading' landscape features, *e.g*. field shape, to assess the origin of the hedgerow. Barnes & Williamson (2006) indicate that hedgerows along roadsides, particularly those with ancient origins (*e.g*. the A15, bordering University of Lincoln farmland, which traces the Roman's Ermine Street), may prove to be the oldest. In General terms any hedgerow in which hawthorn predominates with blackthorn (*Prunus spinosa*), ash (*Fraxinus excelsior*), dog rose (*Rosa canina*) and quantities of elder (*Sambucus nigra*) and/or maple (*Acer campestre*) are likely to be a result of Enclosure, a legal process which began in 1603, although the great majority of Enclosure Acts were between 1760 and 1820 with most probably dating from the early 19th century. Dates of enclosure may be established with

some certainty from local records, and on occasion there may be an estate record of purchases of plants for hedgerow planting. A reasonable assumption to make in the absence of clear evidence from records may be that the majority of mature hedges, particularly in the farmed Lincolnshire landscape, date back to the Enclosures of 200 or so years ago (as suggested by Tinker, 1974). Good *et al.* (1990) indicated that the ageing process for hawthorn depends on the density of planting and that growth rates vary considerably between sites, making it impossible to age specimens from girth with any accuracy. By contrast, the age of newly-planted hedgerows may be more readily established, whereby precise dates for plantings can be derived from a farm's environmental records.

2.2.4. Hedgerow plant diversity and invertebrate diversity

Habitat maturity needs also to be considered in the context of other aspects such as plant species mix – botanical diversity - which may or may not be linked the ageing process/colonisation. Kennedy & Southwood (1984) and Alexander *et al.* (2006) indicate that hawthorn is favoured by a wide variety of invertebrate fauna, although Toft & Lovei (2000) observed that Common hawthorn (*Cretaegus monogyna*) hedges had lower species richness of ground-active spiders than either white spruce (*Picea glauca*) or rowan (*Sorbus intermedia*) hedges. French & Cummins (2001) showed that the diversity of herbivorous insects of hawthorn (*Cretaegus* spp.) was modest compared with other hedgerow plant species, such as blackthorn (*Prunus spinosa*). Planting hedgerows with high proportions of hawthorn therefore probably has a complexity of effects on different components of the invertebrate assemblages. Natural England/Defra/Forestry Commission (2015) recommendations suggest that no single species should make up more than 70% of the total, although "if the landscape is characterised by a single-species then the planting mix should reflect this", but if this is not the case then one of either hawthorn, blackthorn or hazel "should make up *at least* [my italics] 70% of the planting mix". However, despite the emphasis on planting a mix of different plants, since the majority of herbivorous invertebrates, including most rare species, feed on common plants, botanical diversity is possibly secondary in importance to structural factors for many taxa (Kirby, 1993).

2.2.5. Hedge structure and invertebrate diversity

Research into the importance of hedgerow structure for biodiversity covers both the influence of growth form and also structure achieved through manipulations such as cutting, laying and coppicing. For example, studies on the use of farmland hedgerows by

birds have examined the influence of structure (density, basal area) and length of hedges as well as the presence of other features, such as diversity of tree species, presence of dead timber, proximity to well-vegetated banks and ditches, scrub cover, etc. (*e.g.* Sparks *et al.*, 1996; Hinsley & Bellamy, 2000), all of which may influence the availability of invertebrates. Kirby (1993) emphasized the importance of varied vegetation structure to invertebrates.

Work on invertebrates tends to look at defined, individual taxa. Sparks *et al.* (1999) looked at the influence of field boundary structure on butterflies and monitored the effects of hedge-free versus hedged verges and green lanes on richness and abundance. Green lanes were preferred habitat, which was attributed to their superior floristic richness and sheltering capability (although the importance of management for all types of boundary was highlighted). Griffiths *et al.* (2007) found that heterogeneous boundary habitats, including degraded hedgerows, were of importance to a variety of Carabid and Staphylinid beetle species, whereby generalist predators favoured fence habitats and species vulnerable to disturbance were more likely to be found in degraded hedges. Griffiths *et al.* (2007) advised caution with regard to hedgerow restoration under AES, on account of the possible disruption of assemblages which may be dependent on remnant/relict hedgerows. Using butterflies as indicator species, Oliver *et al*. (2010) also underlined the importance of retaining habitat heterogeneity to ensure insect population stability. This may include habitats not currently thought of as conservation-worthy (Griffiths *et al*., 2007).

As hedgerow habitats mature they become larger, although this is controlled to an extent by management activity. A large population of a plant is found and colonised more easily and so more likely to support a greater diversity of invertebrates than a small one (Kirby, 1993). In addition, the greater the size, the greater is likely to be the complexity and variety of structure with scope to provide living conditions for a greater number and variety of invertebrates (Kirby, 1993). This is in keeping with the main theories of species-area relationships or 'island biogeography' (MacArthur & Wilson, 1967), which is firmly established in ecology (Hanski & Gyllenberg, 1997), and has been applied to 'true' islands but also widely to 'habitat islands' (Speight *et al.*, 1999). Indeed Speight *et al.* (1999) indicate that 'many' studies have shown that the area occupied by a particular plant species is the most important determinant of insect species richness. The species-area relationship has been shown to strongly influence faunal diversity (Speight *et al*., 1999), although it rarely explains more than 50% of variation in insect diversity. Leather (1986) studied a

range of insect fauna of Rosaceae (including hawthorn) and concluded that the most important predictor of species diversity was plant abundance, although some measure of architecture was also a significant factor.

Mercer *et al.* (1999) examined the influence of hedge structural characters on hedge ground flora, including the occurrence of shade tolerant species with increasing physical size of hedge. Their observations suggested shade is an important determinant of variation in species composition of hedge floras (and therefore also likely invertebrate fauna), suggesting further investigation. Other research has focused more on hedgerow size and structure and suggests that there is a need for further examination of the effects of differences of hedgerow size, taking into account diversity of cutting stages and management practices, particularly under Stewardship (Bates & Harris, 2009; Bealey *et al*, 2009). The influence of hedgerow management on botanical and faunal diversity has most recently been addressed by work at the Centre for Ecology and Hydrology (Staley *et al.*, 2012b; 2015; Amy *et al*., 2015).

In addition to the hedgerow itself, structural variety at ground level is also an important consideration when evaluating the quality of a habitat for invertebrates. Kirby (1993) emphasized the importance of different heights of vegetation and also areas of bare ground, since bare ground amongst sparse vegetation not only gives access to warmth but also provides space that enables movement, access to resources and colonization.

2.2.6. Evaluation of hedge structure

Structure is defined in some studies (*e.g.* Pollard & Holland, 2006) as consisting of no more than height, width of hedgerow and width of margin or herbaceous base either side of hedgerow. Other essentially 'structural' features, such as 'connectivity' with other habitats, have been shown to be important in other studies (*e.g.* Gruttke & Willecke 1993). Survey methodologies, such as Defra's standard procedure for hedgerow surveying (Defra, 2007), or HEGS (Hedgerow Evaluation and Grading System) an earlier precursor, are useful in assessing and evaluating structural elements (reviewed by Rich *et al.*, 2000). HEGS is an evaluative technique based on a scoring system designed to assess the overall ecological value of the hedgerow, based on features such as height, width, *etc.* (Clement & Tofts, 1992), but seems not to have been widely used.

Certain studies use other more novel measures or 'surrogates' for structural quality, such as optical porosity. Lazzaro *et al*. (2008) tested the efficiency of hedgerows as a barrier to spray drift and defined porosity to be the level of visibility beyond the hedgerow.

This was measured by stretching a white sheet behind the hedge and analysing the amount of white showing through in high-resolution digital photos of the hedges. Amy *et al*. (2015) used a similar technique to assess hedge 'gappiness', processing images with software which assigned pixels to binary categories of 'hedge' or 'gap'. Porosity has also been measured in a similar way for forest canopies using digital photography and hemispherical silhouettes (Zhu *et al*., 2003). The use of light measurements (in Lux) to assess shade and hence hedge density, have been outlined by Sustek (2008).

Sparks *et al.* (1996) proposed hedge 'volume' as an explanatory 'structural' variable, which can be relatively easily calculated from measurements of width and height along the boundary in question. Research by Burel (1992) on Carabid assemblages in hedgerows underlined the need also to look not only at the structure of single hedges or sections of hedges in isolation but to take note of the structure of the 'network', including the extent of 'connectivity'.

2.2.7. Hedge management and agri-environment schemes

Since most AES money has, until recently announced changes, been directed towards hedgerow management rather than new planting, Defra has been most interested in studies which are able to demonstrate, preferably through experimental manipulation of hedgerow structure, the influence of different cutting/trimming and other management regimes (including non-intervention) on a variety of wildlife, including invertebrate taxa (IACR, 2000; Barr *et al.*, 2005; Staley *et al*., 2012a, 2012b; Amy *et al*., 2015).

Defra (MAFF) project BD2102 (IACR, 2000) ran from 1995 to 2000 and examined the effects of management, including flail cutting. It found that the response of invertebrate groups to the hedge being cut in either winter or spring was complex, with different taxa responding in different ways. It also found that hedge laying can encourage a diverse range and high abundance of invertebrates as the hedge grows.

In 2008, Defra commissioned the CEH to investigate the influence of cutting regimes under environmental stewardship on hedgerow botanical diversity. Initial results include an assessment of the effectiveness of different cutting regimes on the berry crops of farmland hedgerows with recommendations to relax cutting frequency (Staley, 2012b). A review of hedgerow floral diversity has also come out of the project (Staley *et al*., 2013). There currently appears to be relatively little published material (aside from a small number of Defra-funded studies and reviews) on the effects of or benefits of AES hedgerow measures with regard to invertebrate diversity. This is despite commentators and

interest groups such as Hedgelink calling for further recognition of the breadth of importance of hedgerows, particularly functional diversity (as a safe harbour for pollinators and pest control species) and other 'ecosystem services', such as pollution control, carbon storage, *etc*. (Bealey *et al.* 2009).

Evidently certain research topics identified some time ago as in need of redress still have not been tackled. Staley *et al.* (2012a) cited Barr *et al.* (2005) who called for further investigation into taxa other than the more usual butterflies, bumblebees, Carabid beetles, Staphylinid beetles and spiders. Deeming *et al.* (2010) studied a broad spectrum of invertebrate populations in the hedge bases of stewardship hedgerows, but broader faunal surveys of hedgerows under AES are relatively infrequent in published literature (Randall & James, 2012). Notable recent additions to that body of work, have come from the research group at CEH, who have investigated the effects of hedgerow management on wildlife and in particular invertebrate community structure (Amy *et al*., 2015; Staley *et al*., 2015). Amy *et al.* (2015) demonstrated the benefits to invertebrate abundance of a range of rejuvenation techniques, notably different cutting and hedge laying regimes. These included methods described as 'reduced labour', such as a form of mechanical laying, which yielded the greatest abundance for all trophic groups than other forms of management. However, interestingly, treatments performed no better than the unmanaged control, once data were scaled for hedge height.

Adoption of such rejuvenation techniques may be limited by the willingness and the capacity of farmers and their contractors. They are voluntary measures most suited to Higher Level Stewardship, whereas there are more farmers for whom this level of Stewardship is not an aim or even attainable. Perhaps hearteningly there is some evidence that even the very basic Entry Level Stewardship options for hedgerow planting and management can be effective and cost-efficient compared to other more extensive and demanding options, at least to certain taxa such as pollinators (Hodge & Reader, 2010).

There is nonetheless a continued need to monitor what is achieved in practice through environmental measures, and the effectiveness of Stewardship in creating and maintaining a hedgerow stock of quality and value to a wider diversity of fauna. We should reward landowners for planting hedgerows to achieve environmental benefits, but we should make at least part of the payment dependent on successful outcomes. In this way there is a real and not merely an imagined benefit to the environment and to ensure that the taxpayer achieves genuine value for money (Davis, 2014). We also need to find some encouraging news for farmers and policy-makers to show that efforts to establish and

protect these habitats are worth it and can show tangible results. How we measure the success of outcomes, particularly for the invertebrate fauna is a key question.

2.3. Sampling and surveying techniques for hedgerows

Remote sensing has provided good evidence for the magnitude and rapidity of habitat destruction, using radar images rather than optical images to give a high precision view of both the extent and structure of habitats. Such techniques have been used to characterize the structure and condition of hedgerow networks (*e.g.* work in France by Betbeder *et al*., 2014). Although these techniques are capable of showing fragmentation in hedgerow networks with very good accuracy at a landscape scale, they cannot, however, tell us about the potentially important smaller scale 'detail' of habitat quality and structure nor the effects on fauna, which remain largely cryptic (Dirzo *et al*., 2014). Hence, despite advancements in technology in ecology, there are still areas where more labour-intensive, less technological approaches are required to survey and sample flora and fauna.

2.3.1. Invertebrate sampling techniques and their effectiveness

The variety of trapping techniques applied to hedges, both at their bases and their canopies, reflect the necessity to employ procedures that suit different habitats, objectives and/or taxa (Southwood & Henderson, 2000; Hill *et al.*, 2005; Sutherland, 2006), as well as personal choice. Taxa may differ in their 'trapability' and different habitats may require different or even novel approaches. The sheer variety of methods applied to sampling invertebrates in hedgerows, makes an assessment of effectiveness and comparisons with the results of other work on hedgerows difficult. All types of sampling will be subject to some extent to variation in catch rates in response to time of trapping and weather.

Natural England provide wide-reaching and instructive practical guidance on invertebrate surveillance (Drake *et al*. 2007). Advice ranges from number of replicates, number of visits and their timing (4 or 5 visits between May and September), suitability of trap types for different taxa and different habitats, equipment needs. Duelli *et al.* (1999) offered advice on the types of traps most suitable for capturing diversity in agricultural field work, recommending several techniques in combination, in addition to optimised selective sampling periods, rather than continuous sampling. Oliver & Beattie (1996) also recommended 'optimised' single session (3-week duration) spring and summer pitfall trapping as being most representative of more intensive sampling.

Pitfall traps are widely used for surveys of ground-active invertebrates in agro-ecosystems, including semi-natural habitats such as field margins and hedgerows (*e.g*.

Biaggini *et al.*, 2007; Deeming *et al.*, 2010; Pywell, *et al*., 2011). However, although protocols for pitfall trapping are well-established (Sutherland 1996; Sykes & Lane, 1996; Southwood & Henderson, 2000; Hill *et al.*, 2005), they are not standardised with respect to trap size, intervals, *etc.*. There are numerous caveats attached to use of pitfalls (*e.g.* Adis, 1979; Southwood & Henderson, 2000; Drake *et al*., 2007), including: digging-in effects; differential effects of preservatives on catches, *e.g*. antifreeze seems to "work better" for Carabids, while water produces different catches; and also differential capacity of invertebrates to escape, by exploiting minute 'footholds' created by minor imperfections or damage to internal surfaces of traps. Duelli *et al. (*1999) suggested that pitfall traps should not be relied on in biodiversity evaluation since, while epigeal predators (notably Carabid and Staphylinid beetles and spiders), which are well-represented in pitfall catches, are excellent indicators for habitat quality in terms of biological control of pest organisms, they make poor correlates for overall organismal biodiversity. Duelli & Obrist (1998) recommended the use of several collecting methods – notably flight traps (window and pans) and pitfalls (funnel and cups) – in field investigations in order to get an 'indicative' view. They concluded that biodiversity correlations are "usually much better for flight trap data", even though pitfall traps often collect many more individuals. In addition to pitfall traps, Pywell *et al*. (2011) employed a range of techniques (Butterfly Monitoring Scheme (BMS) transects, sweep netting and soil cores) to monitor the effects of ecological restoration in field margins on invertebrate diversity.

Sampling invertebrates in hedgerow canopies is trickier. Maudsley (2000) proposed fogging or D-Vac suction sampling of hedgerow invertebrates to try to overcome the awkwardness and impracticality he identified as barriers to researching the woody part of the hedgerow. In a subsequent study of hedgerow arthropods, Maudsley *et al.* (2002) used a beating method to sample overwintering predatory arthropods from a single hedgerow: effectiveness is difficult to gauge from this study, due to the time of year of sampling and also because only limited data for spiders is reported for the beatings from foliage. Pollard & Holland (2006) devised their own chemical knockdown or fogging protocol and Amy *et al*. (2005) used a variant of a beating technique similar to that used by Maudsley *et al*. (2002). A fogging approach using short-acting chemicals is capable of giving more comprehensive results than other more selective techniques, such as beating alone or sweeping or line transects. Depending on responses of invertebrate taxa to pyrethroids, beating and hand searching may nonetheless be necessary to dislodge more cryptic organisms. Drake *et al*., (2007) recommend a combination of beating, sweeping and visual

inspection for sampling arboreal assemblage types (complex tree and shrub habitats, although not explicitly hedgerows).

Sticky traps are commonly used to passively sample invertebrates (Anteau & Sherfy, 2010), particularly in monitoring and controlling pest populations (*e.g*. Oecos products[5]). However, some commentators do not recommend its use for biodiversity assessment purposes (Marshall *et al.* 1994). Catch rates may vary diurnally and in response to weather (Anteau & Sherfy, 2010), in common with other sampling techniques. Sticky-trapping is not covered by Natural England's guide to surveying invertebrates by Drake *et al.* (2007), and is not included amongst methods for ecological census/biodiversity surveying of invertebrates by Ausden & Drake (2006) or Hill *et al*. (2000). Where the use of sticky traps is described it is generally in the context of sampling flying insects (*e.g.* Chalmers & Parker, 1989) and is a widely used technique for monitoring targeted invasive or pest insects, such as aphids, moths, *etc*. Southwood & Henderson (2000) discuss sticky trapping technique and its efficiency for capturing winged insects, *e.g.* aphids, leafhoppers and flies. They found flat sticky traps to be less efficient than cylindrical traps or water traps in an aerial environment. Usefulness for other invertebrate taxa seems not to have been well reported, although Gardiner *et al*. (2009) used sticky traps for sampling ladybird populations. Landcare Research (2010) recommends use of prepared commercial traps for ease of use and indicates their capability to capture larger, stronger insects such as honeybees, cicadas, and occasionally bumblebees. Substances and also colours used in sticky traps will have differential effects on catches due to differential responses of insect taxa. For example, yellow glue boards/ paper are known to be attractive to many types of flying insects and are sold commercially to trap aphids, thrips, true flies and whiteflies, *inter alia*, for monitoring purposes (Oecos, 2009).

2.4. Measuring invertebrate biodiversity

2.4.1. Invertebrates as bioindicators

Bioindicators include biological processes, communities or species and are used to assess the environmental impact of both man-made and natural change over time (Holt & Miller, 2010). Terrestrial invertebrate bioindicators have a number of uses: for example, to indicate environmental conditions, such as the composite biodiversity index of

[5] See http://www.oecos.co.uk/index.htm. Products include ready-made wet and dry sticky traps, trapping systems and sticky materials such as OecoTak glue which can be used to tailor-make traps.

butterflies, moths and ground predators employed by the UK Environmental Change Network (ECN) as a climate change indicator; to detect ecological change in human land-use (*e.g.* Andersen *et al*., 2002); to indicate the success of ecological restoration and/or conservation value of a habitat (*e.g*. Gruttke & Willecke, 1993) and quality of landscape characteristics (*e.g.* Biaggini et al., 2007); or be used as surrogates for other species in assessing the ecological diversity (*e.g.* Biaggini *et al.*, 2007; Brooks *et al*., 2012). Since invertebrates comprise most of the organismal variability in practically all habitats, they are considered good candidates for biodiversity evaluation in agro-ecosystems (Duelli *et al.*, 1999)

The use of invertebrate indicators as substitutes for overall diversity is of particular interest in this study. Taking such a short cut is a seductive approach when examining massively speciose taxa such as invertebrates. Bioindicators may function as short cuts to overall diversity assessment, although this makes certain assumptions about how good a correlate or surrogate one taxon can be for the whole range of taxa. Not all species, or communities can serve as successful bioindicators (Holt & Miller, 2010). Indeed, the practice of using specific invertebrate taxa as effective surrogates or correlates of overall organismal diversity has been widely debated (Duelli & Obrist, 1998; Andersen, 1999; Speight *et al*., 1999). In addition, their use is acknowledged as challenging, due to their abundance, speciosity and general unfamiliarity (Andersen, 2000).

Various invertebrate indicators are in use as surrogates for overall biodiversity in agro-ecosystems, but few have been tested for their correlation with organismal biodiversity (Duelli & Obrist, 2003). Single indicators could give a poor measure of overall biodiversity (Speight *et al*., 1999). Büchs (2003b) showed that although a range of different invertebrate taxa have been used to assess agri-environmental biodiversity - to indicate the 'health' or quality of the landscapes or sites on which they are sampled - they are clearly dominated by studies focusing on spiders and Carabid beetles. Gruttke & Kornacker (1995) assessed hedgerow quality for invertebrate fauna using selected indicators, namely Carabid beetles, harvestmen and spiders. These groups behaved very differently in their colonisation of hedgerow habitats and it was concluded that it is not possible to transfer results obtained for one taxonomic group of invertebrates to another. Duelli & Obrist (1998) also suggested that if surrogates are to be used, then epigeal predators, such as Carabid and Staphylinid beetles and spiders, on their own make rather poor correlates for overall organismal biodiversity in cultivated and semi-natural habitats. Sauberer *et al.* (2004) found that best results in indicating biodiversity have been achieved

with combinations of taxa: vascular plants and birds proved to be the most efficient short-cuts for covering overall species richness, whereas invertebrate taxa (orthopterans, ants, gastropods and spiders) fell some way behind and Carabids showed a particularly weak relationship with species richness, echoing results produced by Duelli and Obrist (1998). Yet Carabids in particular persist as indicators of more general invertebrate diversity (*e.g*. Brooks *et al*., 2012).

Duelli *et al*. (1999) performed a wide-ranging assessment of techniques to evaluate above-ground insect biodiversity in agricultural ecosystems and proposed the use of a 'basket' of taxa, *i.e*. a selection of several taxa rather than single taxon. Duelli & Obrist (1998) suggested alternative taxa, which could be used on the basis of their superior value as surrogates or indicators of biodiversity: they compiled a list of the 'top' indicators which, regarding arthropods, showed Coleoptera, Hymenoptera (including Aculeata) and Heteroptera to show the strongest correlations with overall biodiversity.

Parasitic Hymenoptera have been suggested by Anderson *et al*. (2011) as a surrogate or indicator of the overall arthropod biodiversity of certain agricultural habitats – not in terms of speciosity, which is vast and challenging, but in terms of sheer abundance. For some groups however, *e.g*. Collembola, no conclusions on the significance of correlations could be reached due to lack of available/willing expertise, a general problem with using any speciose group, or any less 'popular' taxon considered 'difficult' or simply less charismatic or aesthetically-pleasing.

2.4.2. Target taxa and taxonomic level for assessment

The total inventory approach to recording biodiversity advocated by Wilson (1987) is an enormous task involving the enumeration of all species (Speight *et al*., 1999). Accurate and comprehensive identification of sampled invertebrates down to species level would require time and money and the efforts of many specialists - Wolton & Vergette's, (2012) project to identify the entire diversity of a single organic hedgerow, including over 1,300 insect species, testifies to this. The relative merits of taking a 'surrogate' single taxon or indicator approach compared with total inventory, and also broader and shallower assessments are discussed by Speight *et al.* (1999). Use of single indicator groups as surrogates for overall diversity is regarded by some as misguided due to a poor correlation between the richness of different taxa (Speight *et al*., 1999) and may lend itself to possibly unrepresentative selectiveness (Duelli & Obrist, 1998; 1999; Duelli *et al*., 2003). For example, until recently, butterflies were the lone representative of terrestrial invertebrates

amongst UK biodiversity indicators (Defra, 2013a), but only account for a small percentage of all species in agro-ecosystems. Pollinators were added as a biodiversity indicator in 2014, currently consisting of over 200 species of bee (Defra/JNCC, 2014). Nonetheless, this represents a fraction of the 24,000 insect species in Britain (Barnard, 2011) and even if only a fraction of these were to be found in farmland hedgerows, the demands on identification skills to make species-level determinations would still be considerable.

Assessment to at least family (if not genus) level is advised by some experts in the field of biodiversity assessment (*e.g.* New, 1996; Lee, 1997; Gaston, 2000). Although the taxonomic sufficiency of analysis at levels higher than species is contentious (*e.g.* New, 1996), it does represent a more manageable approach for assessing the diversity of a group of organisms consisting of tens of thousands of species and whose taxonomic literature is acknowledged to be challenging to non-specialists (New, 2005a). Choosing a higher substitute taxonomic level (*e.g.* commonly family or genus – or even order) might not have the fine-grain precision of species identification, but could and would enable characterisation of the biodiversity of the broad spectrum of invertebrates whilst limiting cost, time and expertise constraints. Biaggini *et al*. (2007) have found that order-level assessment of invertebrate communities can discriminate between different land uses (*e.g.* grass strips and woodlots) and could have a use at least in initial rapid biodiversity assessment in agricultural landscapes at local scale. McAdam *et al.* (1994) successfully used order richness to distinguish between the effects of different hedgerow management techniques on invertebrate assemblages. Deeming *et al.* (2010) were able to demonstrate the successful use of higher taxonomic level data (largely order) in distinguishing between hedgerows of differing maturity. Harrington *et al.* (2010) make some important observations concerning declines insect populations in the farmed environment: even within speciose groups such as Diptera there is evidence of increasing dominance of the fauna by a few 'successful' species. While this may be of concern with regard to losses in diversity, it also suggests that a 'reductive' approach to measuring diversity such as the order-level assemblage evaluated here, is not without its merits, especially when operating in an ecosystem in which in any case speciosity may be reduced.

New (1996) suggested that it may be more productive (even than identification down to family or genus) to interpret a limited number of taxonomic groups properly (*i.e.* to species level) than to interpret everything superficially. Many invertebrate groups are however in themselves highly speciose: Barnard (2011) indicates that Diptera and

Hymenoptera, the two largest orders in Britain, each comprise 7,000 species. Taxonomic expertise and the time of those experts is however limited. A possible avenue may be to take a selection of speciose orders and identify at most to family level (covering a range of trophic groups), rather than making determinations down to species level, *e.g*. Joyce *et al*. (1997), Pollard & Holland (2006) and Amy *et al*. (2015).

Balmford *et al.* (1996) have indicated that the lack of precision in predicting species richness may not be particularly important if the goal of higher-taxon usage is simply to compare the relative diversity of sites. It is not within the scope of this study to make a full inventory of hedgerow species, but to investigate faunal composition and structure in order to determine differential responses between types of hedgerow. Where the objective is to examine patterns or rank sites according to invertebrate assemblages then a higher taxon approach is deemed reasonable by a number of studies (*e.g.* Gaston & Williams, 1993; Heino & Soininen, 2007), although often with the caveat that analysis at least to family level should be undertaken. However, Biaggini *et al.* (2007) found a better correspondence between Carabid species diversity and order-level diversity for arthropods than between beetle family- and species-level diversities.

In addition to taxonomic assessment of invertebrate diversity, a functional approach to assessing biodiversity is familiar in the context of agricultural entomology. It is something that the farming community can identify with, and is an approach that has been used in studies of hedgerow invertebrate communities (Pollard & Holland, 2006; Griffiths *et al*., 2007; Amy *et al.*, 2015). A focus on functional diversity might lead us to classify taxa in terms of whether they are considered as more or less beneficial in an agricultural context, as predators, detritivores, herbivores/pests, parasitoids, pollinators, *etc*. However, A strictly functional approach to diversity may be complicated by the fact that invertebrates can show a duality at different life stages, *e.g.* Lepidopteran caterpillars may fit the herbivorous pest category, whereas adult moths and butterflies themselves may contribute to pollination. Taxa may be polyphagous as adults, *e.g.* certain Lygaeidae (ground bugs) are both predatory and seed-eating (Chinery, 2007). Categorising assemblages of hedgerow invertebrates into functional groups may also overlook taxa with perhaps a more ‘neutral’, cryptic or maybe under-acknowledged role, such as barkflies (Psocoptera), whose ecosystem function may be unclear, but which nonetheless have an existence value *per se* (Primack, 2004), and have been subject to calls for further investigation (Barr *et al.*, 2005; Staley *et al.*, 2012a).

For some influential commentators, such as Wilson (1988), the concept of biodiversity implies a 'holistic' view of nature (Faith, 2008), therefore a method that takes into consideration a broad view of taxonomic groups rather than a single taxon approach may be appropriate. Wilson's (1987) ultimate aim of an entire inventory seems idealistic unless the continuing problem of training and funding invertebrate taxonomists is addressed[6]. The problem of how to monitor variation in invertebrate biodiversity (Speight *et al*., 1999), and how to evaluate the outcomes of agri-environmental conservation measures in supporting that diversity, remains. Compromises therefore seem inevitable. Using a range of taxa in a broader and shallower approach, such as advocated by Biaggini *et al*. (2007), may be one answer in bringing us closer to knowing what variety we have, if not how to value it.

2.4.3. Use of biodiversity measures

Measuring biodiversity requires us to take into account not only how many taxonomic groups are present but also their abundance. How to adequately measure biodiversity is a much-debated topic in conservation biology and ecology (Guiasu & Guiasu, 2012). In order to compare results of sampling from different habitats or land uses many so-called diversity indices or measures have been developed over time (Spellerberg & Fedor, 2003). Indeed biologists have been creative in developing indices of diversity, many of which have been proposed. Ricotta (2005) refers to a "jungle" of biodiversity measures but few are widely used, the best known being Simpson and Shannon, both imported into biology from other disciplines (Keylock, 2005; Guiasu & Guiasu, 2012). With so many biodiversity measures to choose from, guidance from Magurran (1988 & 2004) and Magurran & McGill (2011) is valuable, because rather than merely presenting alternative methods they provide a comparative evaluation of applicability and usefulness.

Magurran (2004) makes a variety of alternative recommendations, although she does not confine herself to one 'standard' measure. Use of species (or other taxon) richness, the most fundamental or "iconic" measure of diversity, is widespread and the least controversial option, but does not account for abundance as diversity indices do. Magurran (2004) strongly recommends only the Simpson index for measuring evenness and "heterogeneity", and Berger-Parker (for its simplicity) for measuring dominance (Magurran, 2004). Magurran (2004) and McGill *et al.* (2011) provide comprehensive guidance to the use of a still growing range of techniques to measure diversity. It is clear

[6] A problem highlighted at the Invertebrate Link (JCCBI) Symposium, September 2015

that ‘fresh approaches’ are appearing regularly, and yet Magurran herself (2004) indicates that some of the old diversity indices, *e.g.* Berger-Parker, Simpson, are the best and most easily interpretable. Berger-Parker also has the virtue of being easy to calculate as well as feeling instinctively meaningful and fitting to describe agricultural assemblages, which can be dominated by a small number of highly abundant taxa, but should be used on the proviso that numerical dominance does not equate to ecological importance (Wallwork, 1976).

The Shannon index despite being perhaps the most widespread diversity index in use (Spellerberg & Fedor, 2003) is not the index of choice for many commentators (cited by Magurran, 2004). Amongst the objections is that the Shannon index is difficult to interpret, at least for single sites, although Magurran does admit it is likely to persist and is being used in many long-term investigations as a benchmark measure. Other commentators are more positive about the persisting use of Shannon as a diversity measure.

Jost (no date) opposes the sole use of measures of species richness *per se* on the grounds that they are “the least ecologically meaningful measures of diversity, because they give vagrants and very rare residents the same weight as the dominant species”. Using species richness alone would lead us to assume that an ecosystem with one dominant species and nine rare species was just as diverse as one with ten equally common species. “To avoid conservation mistakes” Jost *et al.* (2010) recommend Shannon entropy (in its exponential form) or the inverse Simpson as abundance-based measures of diversity when differentiating between sites or partitioning habitats such as forest canopies and understoreys, but also a new similarity measure devised by Chao *et al*. (2008).

Google Scholar™ returns 17,300 results for permutations of “Shannon index” for the past 20 years (1995 to 2015), compared with 16,100 for “Simpson index” and only 1,300 for “Berger-Parker index” in the same period. In addition, I reviewed the proceedings of 4 conferences on topics relating to hedgerows, field margins and other agri-environmental measures (Dover, 2012; Boatman *et al*., 2007, 2010, 2013) and found that investigators of diversity provided data on taxonomic/species richness, but, where a measure of diversity was incorporated, also tended to use Shannon and occasionally Simpson indices.

Species abundance distributions (SADs) which incorporate a graphical plot of taxonomic abundances are appealing for their visual impact, especially when comparing several different habitats or ecosystems: community or community structure in terms of dominance and rarity is immediately apparent. There are different ways to present data

including rank abundance distributions (RADs) or Whittaker plots which appear easy to interpret (Magurran & McGill, 2011). Many approaches to SADs have been proposed, but, again without standardisation and are not often used by comparison with diversity indices. It is considered to be a promising area with more methods emerging, thus increasing the diversity of measures.

Magurran (2004) suggests that scientists could usefully find some common standards in biodiversity measurement to make studies more comparable, but the debate on how best to encapsulate biodiversity, knowing it continues to be an imperfect art, goes on. There is no "true" measure of biodiversity (Hoffmann & Hoffmann, 2008): indices in themselves are a 'proxy', especially because all individuals of invertebrate groups in a habitat or ecosystem cannot reasonably be detected and accounted for. Even when using multiple sampling methods, there may be taxa which prove genuinely rare in absolute terms and not just hard to capture.

Ultimately, choice of diversity measure becomes a matter of personal preference. It is considered legitimate to incorporate several diversity measures in one analysis, since each places different emphasis on common or rare taxa (Jost, no date; Keylock, 2005). In this study, a number of diversity measures have been employed to compare and evaluate any differences between the invertebrate assemblages of hedgerows of different age.

Chapter 3. General Methodology

3.1. Hedgerow types

The study compared the invertebrate fauna of mature ('Mature') hedges (>50 years old) with those recently planted under agri-environmental schemes (AES) during the last 15 years ('New'). By definition these two broad age groups of hedges differ in size and structure (Fig. 3.1), with mature hedges tending to be taller and shrubbier, and young or 'new' hedges forming smaller, less shrubby habitats. New hedgerows (and newly-planted gapping up) can best be identified not only by their stature but also by tree guards which can remain in place for many years helping to support and protect the stems from browsing animals (such as rabbits, hares and deer) as the habitat matures. In this context the hedgerow includes not only the body of the hedgerow, the woody element, which has been planted and managed under AES, but also the hedge bottom which is essentially part of the field margin, *i.e.* the strip of uncropped usually grassy land running parallel with the hedge itself (Figs. 3.2 & 3.3). There is a compulsory requirement (not an AES option) for a 'protection zone' margin of at least 2m from the base of the hedge (Defra/RPA, 2012), which must be maintained to fundamental environmental standards, *i.e.* Statutory Management Requirements (SMR) and Good Agricultural and Environmental Conditions (GAEC) in order for the farmer to qualify for financial support from government funds. Farmers must not "cultivate or apply fertilisers or pesticides to land within 2 metres of the centre of a hedgerow" and must take "all reasonable steps to maintain a green cover" in the 2m protection zone (Defra/RPA, 2012).

There is no real official definition of a hedgerow in the Hedgerow regulations and Natural England (2010) merely describe a hedge as "a line of bushes". Defra's Hedgerow Survey Handbook (2007) is a little more precise defining a hedgerow as "any boundary line of trees or shrubs over 20m long and less than 5m wide at the base, provided that at one time the trees or shrubs were more or less continuous". The Rural Payments Agency (RPA) also uses "a continuous length of at least 20m" for guidance in its advice and inspections. All hedgerows included in this study met these basic criteria relating to length and width.

3.2. Locations and hedge selection

Locations and hedgerows were selected largely on 'non-probability sampling' (Trochim, 2006) rather than random basis, *i.e*. convenience and practicality were major considerations. Choices were thus based on a pragmatic approach that reconciled the willingness of landowners to participate with what was accessible and practically possible by a single researcher.

Four locations were used as sampling sites:

- The University of Lincoln's own farmland at Nettleham (centred around Ordnance Survey Grid Reference TF0566) and Riseholme (centred around SK9875);
- Sir Richard Sutton's Estates in the Lincolnshire Wolds at Swallow (centred around TA1703), with which the University already had an established relationship; and
- Potterhanworth (centred around TF0566), whose contact details were obtained via Natural England. Natural England had pre-selected the farm, indicating that the farmer was particularly 'open' and ecologically engaged and had already participated in student projects.

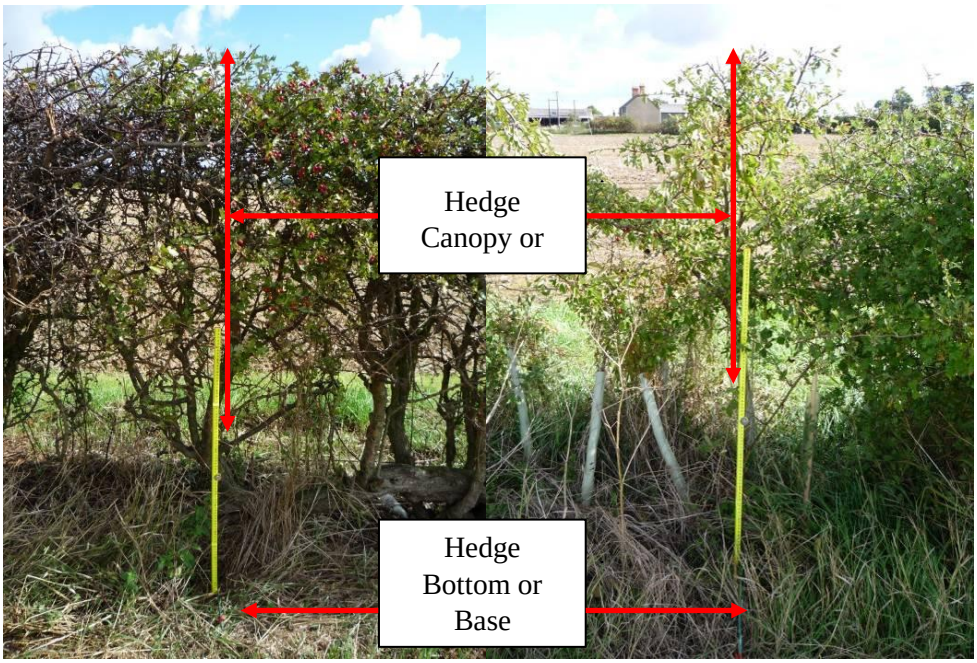


Figure 3.1. Comparison of basic structure of Mature and New hedgerows (photographic examples from University of Lincoln farmland). A Mature hedge is shown on the left and a 'New' hedge on the right complete with white tree guards. The vertical yellow stick measures one metre. This is for illustrative purposes only, as not all hedgerows conformed to these dimensions

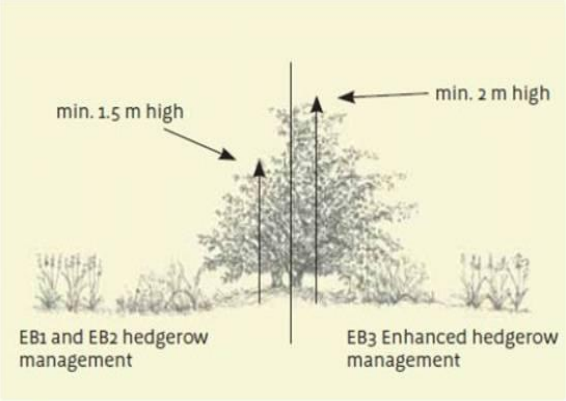


Figure 3.2. Schematic diagram of the cross-section of a hedgerow. A vertical line marks the centre of the hedgerow, and the 'protection zone'/margin is shown in profile. The minimum requirements for hedge height are shown and the main hedgerow options for Entry Level Stewardship are indicated: EB1 = management on both sides of the hedge, EB2 = management on one side of hedge, EB3 = Hedgerow management for landscape and wildlife. Source: Natural England, 2010. © Natural England/Charlotte Lemmon

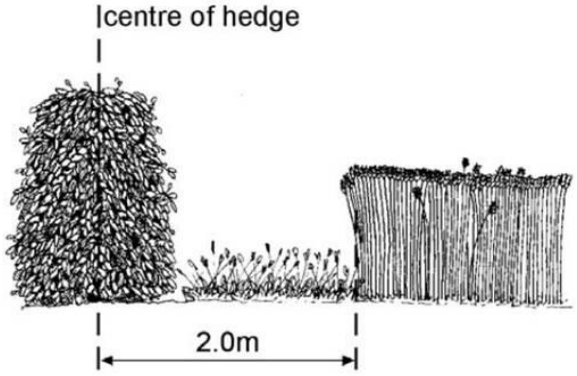


Figure 3.3. Schematic diagram of the cross-section of a hedgerow, showing the 2 metre protection zone which must be protected from incursion and pollution under basic Cross compliance (GAEC 14). Source: RPA, 2011. ©Richard Yardley, Natural England

From across the four farm sites, a total of 36 hedgerows/field boundaries were identified for inclusion in survey work. The hedgerows comprised 16 mature hedgerows (> 50 years of age) and 16 recently planted hedgerows (i.e. less than 15 years of age and planted under AES). The ages of the newly-planted hedgerows were derived from farm records, but for mature hedgerows the matter of ageing the hedgerows accurately was less precise. Historic maps kept at the University, in the local public library and the County Archives enabled dating of only one (c. 50-year-old) boundary, at Riseholme, to within a decade. The rest of the mature boundaries were dated using Hooper's Hedgerow History Hypothesis, *i.e.* as a rule of thumb age is calculated by adding 100 years for every shrubby/woody species found in a 30 yard length of the hedgerow, where a yard is approximately equivalent to 1 metre (Pollard *et al.* 1974). I disregarded shrubs such as Elder and Rose from the calculations because of the speed with which they can establish and focused only on tree species. Hooper's hypothesis is based on an assumption that the majority of old hedges were initially planted as single species rows of a constant recruitment rate to the woody species in the hedgerow of one species per 100 years. The calculation was based on investigations of over 200 hedgerows in a number of counties,

which included Lincolnshire. Hooper himself warned that there could be as much as 200 year margin of error either side of the estimated date for any hedgerow (Pollard *et al.*, 1974). Other hedgerow researchers have also shed some doubt on the usefulness of the hypothesis and a reviewer of early records on hedge-planting concluded that mixed planting was historically far more common than Hooper assumed (Johnson, 1978). Nonetheless, the vast majority of the mature hedgerows were largely Common hawthorn (*Cretaegus monogyna*), rather than Midland hawthorn (*Cretaegus laevigata*), high proportions of which are said to be an indicator of ancient hedgerows (Dowdeswell, 1987). Barnes & Williamson (2006) suggest that a reasonable assumption in the absence of any other records, may be that the majority of hedges standing today could be 200- to 300-years-old (coinciding with the Enclosures of the 19th Century), but are unlikely to be truly 'ancient'.

In addition to the hedgerows, four 'hedgeless' or 'grassy boundaries' without a hedgerow were selected on the basis of availability and accessibility, and close proximity to other hedgerow types at particular farms. One of the grassy boundaries was a beetle bank; the other three were relict hedgerows that had never been replanted. In this context, grassy boundaries are defined as continuous linear field margins of at least a 20m length without shrubs or trees. There is a long tradition of hedgerow boundaries in large parts of Britain's farmed landscape, which combined with the massive programme of hedge-planting that has taken place as part of AES in the last decade or so, meant that field boundaries without a hedge were in general not abundant and not conveniently located.

An inventory of the hedgerows and the 'grassy boundaries' included in the study is shown in Appendix A, Table A1, providing brief details of the location, number, age and dimensions of the habitats investigated.

3.3. Length and location of sampling transect

The central 30m section of each hedgerow was selected as a transect for invertebrate surveying. This choice was based on standardized survey procedures described in Defra's 2007 Hedgerow Survey Handbook (Defra, 2007) which requires a 30m section to be surveyed for specified botanical and structural features. The Hedgerow Survey does not specify that the 30m transect should be at a central point along the hedgerow, but at least 30m away from the end point. Rich *et al.* (2000) indicated that at least botanically 30m transects correspond well with the rest of the hedge and could be seen as representative. Pollard & Holland (2006) sampled hedgerow arthropods at intervals

along the whole length of 13 hedges and found "consistent aggregations in the middle of the hedge", and so by placing the transect in the middle of the hedge length it should be possible to gauge 'aggregations', which in turn presumably represent a point of maximum abundance and diversity along any particular hedgerow, even if this may not be typical for the whole length of hedgerow.

In order to locate the centre of each hedgerow the length of each hedgerow was paced out and measured using the odometer feature of a Garmin etrex handheld GPS device and the latitude and longitude of the midpoint recorded from the Garmin device, with an accuracy of +/- 4m. The centre point was marked for future reference by attaching red tape to a branch of the hedgerow.

3.4. Selection of invertebrate sampling techniques: methods for trapping invertebrates at ground level

A number of different techniques were considered for sampling both the invertebrates at ground level[7] in the hedge bottoms and also the canopy-active invertebrates in the hedge tops. Choice of trapping method was made on the basis of published material and on laboratory and field experiments conducted to test the trapping efficiency of alternative methods.

At the outset, a pitfall trapping protocol to Natural England standards (Drake *et al.*, 2007) was considered the most straightforward and conventional method for sampling invertebrates at the hedge bottom. This method had also been used in a precursor study (Deeming *et al*., 2010), and the intention was to extend the work done in that study, incorporating use of a sticky trapping technique and comparing its effectiveness with pitfall trapping. Fieldwork in April/May of the first year of investigations (2010) however began in very dry weather conditions, with ground so hard that the digging in of pitfall traps became difficult even with the assistance of a bulb planter. Pitfall trapping ceased and a sticky trapping regimen continued, based on desk research, experimental laboratory work and pilot studies undertaken over the spring and summer of 2010 (Appendix A).

Sticky traps can be cheap and easily replicable, and highly effective in sampling invertebrates (Young, 2005). However, invertebrate surveying and censusing guidance generally omits sticky trapping as a technique (Hill *et al*., 2005; Sutherland, 2006; Drake *et*

[7] The term 'ground-active' is not used as many of the taxa collected using sticky traps at ground level in the hedge bottom/grassy boundaries would not normally be considered as such, but clearly do forage, rest, bask *etc* on the ground.

al., 2007), or makes only a fleeting reference (New, 1998), perhaps because it is more conventionally associated with use in monitoring and control of crop pests, such as Hemipterans and Dipterans (*e.g.* Büchs, 2003a; Robacker & Rodriguez, 2004; Hallett *et al.*, 2007), than with biodiversity assessment. Where the use of sticky traps in ecological studies is described, it is most likely to be used for sampling insects in flight, *e.g.* in forest ecosystems, in crop canopies and horticulture and/or single taxon studies (Chalmers & Parker, 1989; Southwood & Henderson, 2000; Young, 2005; Oecos, 2009; Boutin *et al*., 2011). Some use in biodiversity studies is evident, as well as use on the ground as opposed to aerial environments. Thomson *et al.* (2004) tested sticky traps for monitoring invertebrate diversity in viticulture to 'bioindicate' good environmental management, concluding that sticky trapping can be effective in sampling both pest and beneficial species. Boutin *et al.* (2011) used sticky traps to measure the moth diversity of woody hedgerows. An RSPB project investigated the effects of soil moisture content on the abundance of crane flies (Diptera: Tipulidae) using a sticky trapping technique at *ground level* to trap the flies on emergence from vegetation (Matthew Carroll, personal communication[8]; Carroll *et al.*, 2011; Carroll, 2012).

Often sticky traps are used with some kind of chemical lure (Young, 2005), however no baiting was employed in my study, although some bias due to colour (white) cannot be excluded. Southwood & Henderson (2000) discuss sticky trapping briefly in their guidance on population measurement, in relation to its efficiency for capturing winged insects – *e.g.* aphids, leafhoppers and flies. Usefulness for other more 'robust' taxa seems not to have been well reported, although Gardiner *et al*. (2009) used the technique for sampling ladybird populations.

Regarding the choice of sticky trap, Landcare Research (2010) recommends use of prepared commercial traps for ease of use and indicates their capability to capture larger, stronger insects. Landcare's view is that use of (unspecified) readily-available commercial traps is preferable to tailor-made 'home-made' traps, in terms of speed and ease of use. The effectiveness of different types of sticky trap was tested in the laboratory and in the field using commercially ready-made materials (Rentokil™ Advanced Fly Window Stickers, Oecos Delta Traps™, Time's up Insect Catcher™ by STV International, Zero In™ Cockroach traps by STV International), as well as two types of improvised trap

[8]Matthew Carroll was PhD student at the University of York. He presented findings at the Royal Entomological Society Postgraduate Forum which I attended in February 2011.

(Oecotak™ A5 and B&Q Silver Gaffer (duct) Tape), leading to the selection of the Cockroach traps (Fig. 3.4). Principle pilot studies are summarised in Appendix A, sections A1 and A2. For illustrative purposes, different sticky materials used in lab pilots are shown in Appendix A, Figures A5a–e.

Prior to work in the laboratory and field work, Ethics and Risk Assessment forms were completed and approved. Included in the Ethics form was a commitment to abide by a code of conduct for collecting insects and other invertebrates originally devised by the Joint Committee for the Conservation of British Invertebrates (Amateur Entomologists' Society, no date). Risk Assessment covered issues such as working with noxious chemicals and lone working.

3.5. Sticky trap method for sampling at ground level

For use in the field, the Cockroach traps were cut to size (6 x 10cm trapping area, plus narrow 'handling strip' with no adhesive) to fit a demi diamond moth trap holder (Killgerm brand). The demi-diamond trap was designed to be used with pheromone attractants, but the pheromone reservoir was removed from the traps. Figures 3.4 (a) - (f) show the construction of the sticky trap including the protective wire cage.

By-catch of amphibians, small reptiles and small mammals had previously been a concern in pitfall trapping activities and was likewise of some concern in the proposed sticky trapping regime. In pitfall trapping Hill *et al.* (2005) recommend use of wire mesh or chicken wire to reduce the chances of catching non-target taxa, but do not specify a gauge. Drake *et al.* (2007) on the other hand are more specific in their pitfall trapping protocol and suggest a cover of 30mm mesh chicken wire. Avoidance of unwanted by-catch of vertebrates is an important consideration, not only for conservation and ethical reasons, but also in helping ensure sampling effectiveness: capture of non-target animals can disrupt or distort captures of target animals, *e.g.* by attracting predators or decomposers (Pearce *et al.*, 2005; Lange *et al.*, 2011) and also simply by taking up space in the trap itself. Furthermore, when trapping it is necessary to minimise the chances of death or damage to non-target vertebrate species protected under Schedules of the Wildlife and Countryside Act (1981).

A protective cage was devised to prevent 'by-catch' of non-target vertebrates, notably small mammals. Preliminary field work using protective cages of 13mm x 13mm gauge wire mesh had shown that shrews, as obligate insectivores, despite the mesh covers, were susceptible to being caught. This was based on observation rather than extensive

collection of data, since, as soon as it became apparent in field trials that the initial protective cover did not exclude shrews (genus *Sorex*), a new cover was devised. Access by small mammals to traps was prevented by constructing cages using 6mm x 6mm wire mesh. Cages were designed to cover the demi-diamond and measured 20 cm (length) x 9 cm (width) x 5 (height). The wire mesh was cut and bent into shape and closures made from narrow garden/plant wire were used to keep the protective cage shut during trapping. Figures 3.4d–f illustrate the sticky trap and the protective cage cover. Figure 3.5 shows a sticky trap/cage in situ at hedge bottom. Sticky traps were positioned on the ground within the 2m protection zone within ~1m of the hedge centre.

As a result of using this protective cage, it is likely that not only vulnerable small mammals were excluded but also some of the (larger) invertebrates. The very largest Carabid beetles (Tribe Carabini), which can measure up to 35mm in length (Luff, 2007), may have been excluded because of their size. Despite the protective cover, it was nonetheless evident that larger invertebrates, notably larger Carabids (>20mm), could be caught; see Fig. 3.6, which is also illustrative of the range and distribution of animals caught. Invertebrates, such as spiders, may have been disproportionately attracted by the structure: research has demonstrated their attraction to structural complexity presumed to be site-seeking for web attachment (*e.g*. Bultman & Uetz, 1982).

The sticky traps were devised to be placed into habitats rather than being dug in, meaning that sticky traps fulfil the criterion of keeping disturbance and destruction of ground habitat to a minimum, by contrast with pitfall trapping, which involves digging in and for which disturbance effects have long been noted (*e.g.* Adis, 1979).

3.6. Selection of invertebrate sampling techniques: methods for collecting invertebrates from the hedge canopy

Localised fieldwork on University farmland demonstrated that the sticky traps were capable of capturing a diversity of invertebrate fauna at ground-level (Appendix 2), but pilot trials indicated that although they were capable of trapping useful numbers of a range of invertebrates in the hedge bottom, they did not appear to be efficient at sampling the canopy of the hedges (Appendix 2, Fig. A2.1). Other sampling techniques were considered from amongst a range of techniques commonly used to sample invertebrates from aerial environments and woody vegetation: suction sampling, water traps, branch clipping, branch tapping or sweep netting and chemical fogging (New, 1998; Southwood & Henderson, 2000; Hill *et al*., 2005; Ozanne, 2005). Sweep netting was rejected at the desk research stage, because of the desire to sample invertebrates in the hedgerows, not merely

close to the canopy surface. Vegetation clipping may be a way of collecting data on sessile organisms such as scale insects (New, 1998), but because of the potential of damage to vegetation or change to structure was considered unsuitable for repeat fixed transect surveying. Limited manual branch clipping was undertaken, but tended to catch very little barring spiders and results are not presented due to paucity of data.

Fogging with pyrethroid insecticides was used by Pollard & Holland (2006) to perform one-off sampling of arthropods within the woody element of a selection of hedgerows. They justified their use of fogging on account of the complex structure of the hedgerow vegetation, the mobility of arthropods and the fact that hedges remain relatively undamaged by this form of sampling. Although pyrethroids are reckoned to be short-acting, it was considered that the technique might not be suited to a sampling regimen involving repeated visits to the same sections of hedgerow, as opposed to one-time sampling such as that performed by Pollard & Holland (2006).

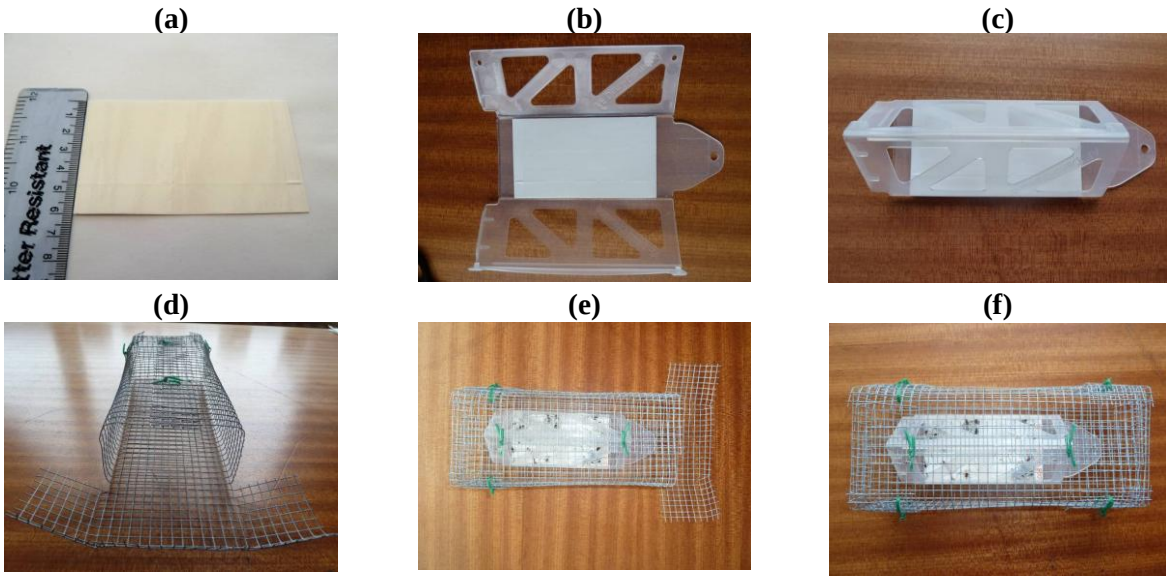


Figure 3.4a-f. Photographs of sticky trap and protective cage, showing: (a) Cockroach trap sticky pad cut to size; (b) sticky pad on adapted demi diamond moth trap holder (manufactured by Killgerm); (c) demi diamond holder with sticky pad closed; (d) wire mesh (6mm x 6mm gauge) protective cage, viewed from narrow end; (e) wire mesh protective cage containing sticky trap seen from above, open at one end; (f) protective cage containing sticky trap seen from above, closed and ready for setting. Garden wire (green) securing cage in a closed position can be seen

Figure 3.5. Sticky trap in protective cage in situ in the field at hedge bottom April 2011

(a)

(b)

Figure 3.6. Photographs of sticky traps illustrating catches: (a) sticky pad from September 2011, highlighting larger Carabid beetle (circled in red on the right) and smaller Carabid (circled in red on the left). Sample is characterised by numerous Opiliones (harvestmen); (b) sticky pad from July 2011 showing range and distribution of animals caught, including Diptera, Hemiptera (notably Leafhoppers), small Hymenoptera (Parasitica) and Isopoda

Figure 3.7. Demonstration of a conventional beating technique showing a beating tray being held up beneath a bush and the collector holding a beating stick. Source: WSU Pest Management Transition Project, http://appleipm.blogspot.co.uk/2011/05/western-flower-thrips-campylomma-in.html

Figure 3.8. Beating funnel illustrating both (a) the original 28cm diameter plastic food funnel, and (b) the enlarged 50cm diameter funnel incorporating dog collar. Collecting containers are also shown

Figure 3.9. Investigator demonstrating the adapted beating technique using 50cm diameter funnel (with collecting container) to sample invertebrates from a domestic Common Hawthorn (*Cretaegus monogyna*) hedge

Beating, or ‘jarring’, entails tapping and shaking off small animals by striking aerial vegetation, such as hedgerow canopies, with a stick and conventionally using a tray for collection of organisms dislodged from the vegetation (Fig. 3.7). The beating technique can be used in pest monitoring, for instance in orchards to test for the presence of organisms such as aphids or spider mites. Beating is also recognised in ecological literature as a *bona fide* method of assessing and estimating invertebrate populations of woody habitats (*e.g.* New, 1998; Southwood & Henderson, 2000; Drake *et al.* 2007). Although often used by collectors to sample invertebrates, beating/jarring does not appear to be widely employed to sample whole communities systematically, and there is little standardisation evident in the literature regarding, for instance, type or size of beating stick, weight of stick, size of beating tray or frequency/duration of beating. There are precedents for using the beating method to collect broader samples from woody vegetation as part of biodiversity surveys, *e.g.* Southwood *et al.* (1979). Maudsley *et al.* (2002) use the technique for sampling overwintering Araneae, Carabidae (Coleoptera) and Staphylinidae (Coleoptera) from a single hedgerow. Beating is known to have been used in recent hedgerow research by the CEH (Sam Amy, personal communication).

Among its advantages, beating is simple and cheap and the equipment easily portable (in comparison with for instance vacuum sampling). It is capable of large catches, including mobile species, although this is dependent on type and structure of habitat and there is the risk of an ‘escapee’ component (New, 1998), which varies amongst taxa. Beating is also weather-dependent and cannot be used if vegetation is wet and is also best avoided in windy conditions. In common with the majority of sampling methods, both terrestrial and aerial, the beating technique may only be expected to provide at best an indicative representation of the diversity of invertebrates living in a canopy habitat; no entire inventory can be expected.

An adapted beating technique was selected to collect invertebrates from the canopies of hedgerows. Instead of using a conventional beating tray (Fig. 3.7), a wide plastic food funnel with attached collecting container was used to collect dislodged organisms (Fig. 3.8; Fig. 3.9). A 28cm diameter plastic food funnel was initially used for sampling, but was subsequently adapted using a canine Elizabethan collar to enlarge the funnel diameter to 50cm in order to increase the efficiency of sampling (Fig. 3.8; Appendix A, section A3). The funnel was inserted directly into a polypropylene food container which contained a piece of cloth impregnated with killing agent. The collecting funnel and

container were held in the lower reaches of the canopy[9] at ~1m height from ground and invertebrates were tapped off canopy vegetation using a beating 'stick' (a folded 1m plastic measuring stick of the type commonly found in DIY stores) to make 10 strikes at each of 8 equidistant points along the central 30m of hedgerows. Containers were removed from the funnel and placed in a cool bag during sampling work, then subsequently stored frozen prior to identification.

Preliminary studies were conducted in the spring/summer of 2010 to establish the effectiveness of the beating technique using the funnel. This included a comparison of the effectiveness of the adapted beating technique with the fogging used by Pollard & Holland (2006) which showed that, irrespective of differences in sampling regimen, dates and locations, the diversity (if not abundance) of invertebrates sampled by the beating technique was comparable. The results of this work are summarised in Appendices A3 and A4.

3.7. Determining sampling regimen – number of samples

Magurran (2004) suggests that 10 replicates or samples may be a useful starting point when determining the optimum number necessary to measure diversity, but with the caveat that 10, although recommended by other researchers, is not necessarily a magic number. Magurran recommends the rate at which new taxa are being encountered, is the best guide to sample size. Choice of the number of traps per session was determined by use of taxonomic accumulation/accretion curves whereby the number of taxa accumulated in sequential trapping sessions is plotted against the cumulative numbers of traps used. Where the curve starts to flatten marks the point at which the taxonomic richness of the assemblage sampled has been "encapsulated" (Magurran, 2004).

The sampling regimen for this investigation was informed by analysis of taxon accumulation from previous studies of farmland hedgerow invertebrates conducted in 2007/2008 using pitfall trapping, in which 10 pitfall traps had been used per hedge transect for 6 differently aged hedgerows (Deeming *et al.*, 2010). To determine number of replicates, taxon accretion rates for spring, summer and autumn seasons were calculated from pitfall data collected in 2007. From this data taxon accretion curves were generated and examined for accretion rates. An accretion curve (Fig. 3.10), based on 10 iterations performed in Excel, is shown for the hedgerow with the lowest taxon richness, indicating a

[9]Buddle (2013) indicates that the greatest abundance of invertebrates is collected in the lower part of the forest canopy as opposed to higher levels.

minimum sampling requirement, *i.e.* the least number of traps needed to 'encapsulate' the range of taxa present. Accumulation flattened out at 8 samples, whereby sampling effort had achieved a maximum possible catch of taxa (Fig. 3.10). Mean % taxon accretion rates for May, July and September 2007 for all hedges indicated that 8 traps would on average achieve 95% of the original catch (Appendix A, Table A3 and Fig. A9).

3.8. Determining sampling regimen - length of trapping session

In September 2010, pilot tests were run to determine an appropriate length of time for leaving the sticky traps 'active' before collection. Two hedges were selected as 'pilots' from those on University of Lincoln farmland, one Mature and one New. A total of 25 traps were placed at equidistant 2m intervals along a section centred on the midpoint of each of the hedges. Groups of five traps, selected at random, were collected after 48 hours and after 24 hours thereafter on each of the following 3 days, *i.e.* they were left active for 2, 3, 4 and 5 days respectively. Taxon accumulation curves were used to help determine a suitable trapping duration (Fig. 3.11). Accretion levelled out by day 4 in the case of the New hedgerows, although such a marked trend was not found in the Mature data. The decision to leave traps out for 4 days was guided by the apparent minimum requirements for capturing the diversity of the less diverse habitat.

3.9. Invertebrate identification and description

Animals were identified while still attached to the sticky cards, simply by placing the open trap beneath the stereo dissection microscope at x90 magnification and below and lit by a cold light source and the microscope's integral light. Animals caught during beating were sorted in Petri dishes and identified using the same equipment. Count data were recorded on paper prior to transfer to a Microsoft Excel workbook

Invertebrates were identified down to Order level principally, following the 'broad spectrum' approach to assessing diversity in agro-ecosystems used by Biaggini *et al.* (2007). Classification down to (Super-) Family level was undertaken in the case of the three most diverse (speciose) groups in the UK (Barnard, 2011), *i.e*. Diptera, Coleoptera and Hymenoptera, to further explore the adequacy and practicability of alternative approaches to a full inventory of species and in particular in relation to discriminating between the diversity of different habitats.

A range of dichotomous keys and other titles from the field of invertebrate and agro-ecology were consulted during the identification work, most notably Tilling (1987), which enables identification of broad taxonomic groups of terrestrial invertebrates. There

was also reference to: Wallwork (1970) on soil and ground-living organisms; Unwin (1981, 1988, 2001) keys on British Diptera, Coleoptera and Hemiptera respectively; Davis (1991) for insects on nettles; Kirk (1992) for insects on Brassicas; Alford (1999, 2011) on agricultural entomology; Wheater & Cook (2003) on invertebrates generally; Chinery (2007) on the insects of GB and Western Europe; and Oosterbroek (2006) on European Diptera. These sources not only provided keys, but also ecological information subsequently used to inform discussion of findings.

Lee (1997) reported that family-level diversities can be very good indicators of underlying species diversities. Accordingly identification below Order level was conducted for the 3 most speciose taxonomic groups in GB (Barnard, 2011): for superfamilies and families of Hymenoptera and families of Coleoptera and Diptera (see Chapters 4 & 5), but not consistently for other Orders/Classes due to time constraints. The principle reference materials were: for Hymenoptera – Goulet & Huber (1993), Chinery (2007); for Coleoptera – Unwin (1988), Harde & Severa (2009); for Diptera - principally, Oldroyd (1970), Unwin's AIDGAP/FSC guide (1981) and Oosterbroek (2006). Diptera were split into two main groups Nematocera (mosquitoes, midges, gnats, *etc*.) and Brachycera (true flies) and then further into family/superfamily as consistently as possible using pictorial guides and dichotomous keys.

3.10. Measuring invertebrate diversity

There are multiple options for measuring diversity depending on the objective – *e.g.* the extent to which populations may be dominated by certain taxa, the level of heterogeneity and whether populations show evenness. Despite the existence of multiple diversity indices, work continues in pursuit of defining diversity to best effect (Magurran, 1988, 2004; Hill *et al*., 2005; Magurran & McGill, 2011), and yet it is acknowledged that some of the old ones are the best, in terms of their meaningfulness and ease of calculation (Magurran, 2004).

Diversity measures were calculated in Microsoft Excel (2007) using invertebrate abundance data according to formulae and methods set out in Magurran (2004). The selection of diversity indices was based in large part on recommendations by Magurran (2004), and also informed by personal choice and knowledge of widespread usage in ecology. The intention was to investigate the diversity values that can be achieved based on broad taxonomic assessments and explore the extent to which diversity measures are concordant in evaluating diversity of the same dataset.

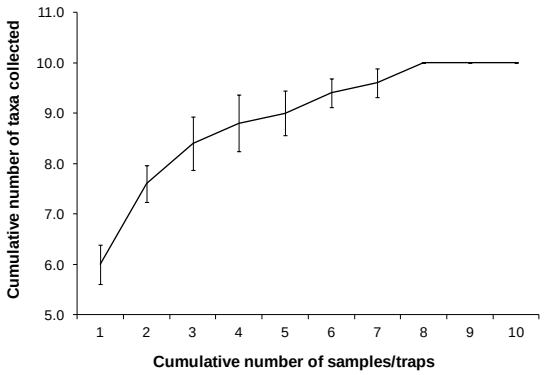


Figure 3.10. Invertebrate taxon (Order/Class) accretion for the hedgerow with lowest taxon richness showing mean (±SE) cumulative number of taxa collected on the y-axis and cumulative number of traps on the x-axis. Invertebrates collected by pitfall trapping in April 2007

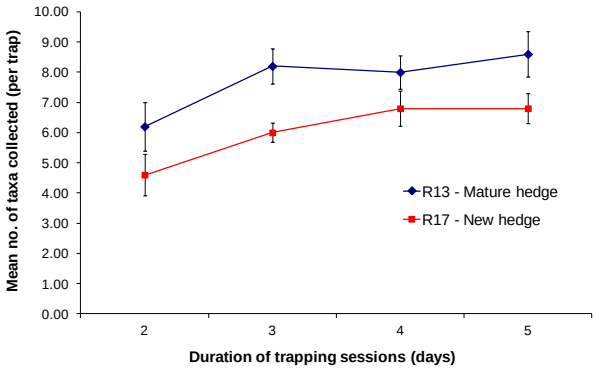


Figure 3.11. Accretion rate of invertebrate taxon richness (± SE) over time for sticky trapping sessions of different durations, comparing one Mature (~100 years) and one New (~5 years) hedge. The y-axis shows mean number of taxa per sticky trap (n = 5). The y-axis shows the trapping session durations (2, 3, 4, 5 days respectively)

3.10.1. Taxon richness

Species richness, or the number of species present in any one ecosystem, represents the oldest, most intuitive measure of biodiversity and is an inventory of the number of species without any reference to abundance. A variant of this most fundamental "iconic" (Magurran, 2004) measure of diversity has been used in this investigation, just as it is often used by investigators as a fundamental measure of diversity as a first step before any thought of generating a diversity index. Biodiversity researchers may confine themselves to presenting a list of species/taxa along with an indication of their abundance, without generating a diversity index, *e.g.* Pollard & Holland (2006). Some biologists in fact mistrust diversity indices because of the difficulty of interpreting even small differences in values produced by essentially nonlinear indices (Jost, no date). In my study, since the level of analysis was not down to species level, the term "taxonomic richness", a count of broad taxonomic groups of invertebrates has been substituted for species richness. The classification into broad taxonomic groups conforms with Tilling's (1987) key, and consists largely of Orders and in one or two cases Classes (notably Chilopoda - centipedes, Diplopoda - millipedes). Collembola, which Tilling (1987) identifies as an Order, are now considered to be a Class (Hopkin, 2007).

3.10.2. Berger-Parker index (*d*)

Magurran (2004) describes Berger-Parker (Berger & Parker, 1970) as an "intuitively simple dominance measure" with the added virtue of being easy to calculate. The index expresses the proportional abundance of the most abundant taxon:

$$d = N_{max}/N$$

where N_{max} is the number of individuals in the most abundant taxon and N is the total abundance. The measure describes the relative importance of the most dominant taxon in any assemblage. I used the reciprocal form of the index (*1/d*) which increases in value as diversity increases and dominance of any one taxon is reduced.

3.10.3. Shannon diversity index (*H'*)

The Shannon diversity index (Shannon & Weaver, 1949) is a measure of heterogeneity based on information theory, with the rationale that the diversity in a natural system can be measured in a similar way to the information contained in a code or message. The index is calculated from:

$$H' = -\sum p_i \ln (p_i)$$

where $p_i = n_i/N_i$ (n_i is the abundance of the *i*th taxon, and N is the total abundance).

Shannon can be seen as weighted towards rare species/taxa. One of the principle objections to its use is that its value may increase as a result of either greater richness or greater evenness, or even both. Consequent issues with interpretation make Shannon unloved by some commentators, but it nonetheless remains one of the most enduring of all diversity measures (Magurran, 1988; 2004), including in reports of farmland invertebrate diversity, *e.g.* Biaggini *et al.* (2007). Many long-term ecological investigations have chosen Shannon as their benchmark measure of biodiversity, so it seems unlikely to decline in popularity, despite its supposed shortcomings (Magurran, 2004).

3.10.4. Simpson diversity index (*D*)

Simpson's index (Simpson, 1949) is a heterogeneity/diversity measure, said to "provide a good estimate of diversity at relatively small sample sizes" (Magurran, 2004). By contrast with Shannon, it is weighted towards the most abundant taxon, while being less sensitive to taxon richness. Magurran (2004) nonetheless calls it "one of the most meaningful and robust diversity measures". The index is calculated from:

$$D = \sum p_i^2$$

where p_i is the proportion of individuals in the *i*th taxon.

As *D* increases in value, diversity decreases, therefore the index is usually expressed as a complement (1-*D*) or reciprocal (1/*D*). The reciprocal was used in this study.

3.10.5. Heip evenness index (E_{Heip})

Heip is an index of evenness derived from Shannon. Heip (1974) believed that diversity measures should have a low value where evenness is low, *e.g.* where the spread of organisms amongst taxa in an assemblage is less even, a lower Heip value will be achieved, and where the distribution of organisms amongst taxa is more even, a comparatively higher Heip value will be achieved. Heip's measure of evenness is calculated using the following:

$$E_{Heip} = (e^{H'} - 1)/T-1)$$

where $e^{H'}$ is the exponential value of H', and T is used by me as a substitute for S, indicating the number of taxa rather than species.

3.10.6. Simpson evenness index ($E_{1/D}$)

The Simpson measure of evenness is calculated by dividing the reciprocal form of the Simpson index (1/*D*) by the number of taxa in the sample (Krebs, 1999). Hence:

$$E_{1/D} = (1/D)/T$$

where T (taxon) is a substitute for S (species). Magurran (2004) recommends the use of this evenness index particularly where Simpson's measure of diversity has been used.

3.11. Collection of explanatory variables

Data for environmental variables were collected in tandem with the invertebrates themselves. Both biotic and abiotic variables were collected as ecosystem attributes potentially explaining the abundance and diversity of invertebrate taxa collected from the hedgerows. Presented here are descriptions only of the variables eventually used in multivariate analysis in Chapter 6. Selection of the factors in the candidate models was made on the basis of correlations demonstrating significant colinearity, *e.g.* field size was found to be highly correlated with distance from woodland and was therefore rejected.

3.11.1. Landscape context

3.11.1.i. Connectivity

As well as providing habitat for a wide range of organisms, including invertebrates, the important of hedgerows lies also in their role as ecological corridors, maintaining the connectivity of the landscape (Chen, 2010; Burel & Baudry, 2012; Hedgelink a & c, no date). This so-called 'connectivity' (or 'connectedness') of hedgerows is considered important because it enables wildlife dispersal, thereby helping preserve biodiversity. Connectivity can be measured in different ways (Chen, 2010). In my study it is measured as the number of other hedgerows that have a direct connection to each end of the hedgerow being surveyed (see the Hedgerow Survey Handbook; Defra, 2007). The Hedgerow Survey Handbook has a tolerance of 20m in defining a connection, but I took a less tolerant approach and counted only those connections that were within 10m (± 4m). There are techniques for measuring connectivity using aerial photography and GIS (Chen, 2010), but the measurements I made were paced out at ground level using a handheld GPS.

3.11.1.ii. Distance from woodland

The distance of the hedgerows from woodland was calculated on the ground where convenient, but largely from Ordnance Survey (OS) maps included in stewardship agreements. The distance was measured between the mid-point of the hedge (on which surveying transect centred) and edge of nearest woodland (no specification on size of woodland was made) as the crow flies. Some distances could be paced out on the ground and measured using the odometer function of a GPS (to ± 4m accuracy). Distance was calculated from the OS maps where pacing out was not possible. Measurements rounded up to the nearest 5m were calculated by drawing a straight line from the edge of the nearest woodland to the central point of the hedge where transects were located.

3.11.2. Hedge and ground vegetation structure

3.11.2.i. Dimensions of the hedgerow – height, canopy width, height above ground

A one-metre measuring stick (see Fig. 3.1) plus an 8-metre metal tape measure were used in the field to measure dimensions of the hedgerow. Where height could not be easily established in the field, notably with the taller hedgerows, photographs were taken including the measuring stick and the resulting images were subsequently analysed, using the measuring stick for guidance and estimates were made from photographs. The metal tape measure was used to gauge canopy width or 'overhang', a one-sided measure of canopy width, whereby the canopy width was measured on the side on which sampling

was conducted from the centre of the hedgerow to the outer edge of the canopy at 1m above ground. Dimensions were based on an average of 8 measurements, taken at 4-metre intervals along the transect (matching the position of the invertebrate sampling points), replicated each month.

Height growth and canopy growth were calculated, derived from the difference between measurements taken in March and measurements taken at the end of August (assumed to represent the beginning and end of the growing season).

3.11.2.ii. Dimensions and structure of the margin – margin width, sward height, margin ground cover

The metal tape measure was used to measure the width of the margin, taken to be the distance from the centre of the hedge to the outer edge of the margin. As before, dimensions were based on an average of 8 measurements, taken at 4-metre intervals along the transect (matching the position of the invertebrate sampling points), replicated each month.

Stewart *et al.* (2001) evaluated quick methods to assess sward height including use of what they call "direct measurement" and use of a "sward stick". The method used in this study is a type of direct measurement using a rigid metal measuring tape. This method of measuring sward height was deemed as being sufficiently accurate to be used to measure both tall and short swards and the only suitable method if sward height is used as a surrogate for microclimate.

Maximum margin sward height was measured using the measuring stick/metal measuring tape. Measures of the maximum sward height were taken at each of the 8 sampling points along each hedgerow transect to the nearest 10cm.

Margin ground cover is a measure of the cover of vegetation and bare patches at ground level. A % measure of cover was used according to a Domin scale which uses broad bands (Hill *et al*., 2005), estimated by eye using a 1 x 2m quadrat (the quadrat size used in the Hedgerow Handbook (2007) survey guidance).

3.11.2.iii. Measuring the density of vegetation – canopy light and ground light

Density/porosity of vegetation in the hedge canopy and hedge bottom has been determined using lux, a measure of visible light conditions, in both the hedge bottom and in the hedge canopy, based on techniques used to measure plant and forestry canopies. Light penetration into the hedgerow and down to ground level was calculated from two sets of measurements of illuminance in lux: one set of measurements was taken within the

canopy of the hedgerow/in the hedge base at the trap site and one set of measurements of the ambient light conditions outside the hedgerow canopy. From these measurements a % light 'penetration' was calculated based on the difference in values between the hedgerow readings and the ambient light readings. In the woody part of the hedge the lux meter was inserted into the hedge canopy at a height of approximately 1m to a depth of circa 25cm at the 8 fixed sampling points (from which a hedge average could be calculated) at which beating was conducted.

Likewise, for measuring the light conditions at ground level, two sets of measurements are taken, one at ground level by the trap and one outside the hedgerow in full daylight. The difference between the two measurements indicated the light penetration, and thereby the density or porosity of vegetation at ground level at the base of the hedge.

All measurements were taken with a Tenmars TM-201 handheld lux meter with a silicon photodiode and filter, normally used to assess light conditions in industrial and office environments. The lux meter did not log data automatically but had a hold function enabling readings to be taken from a screen and recorded by hand. Ceptometers are conventionally used to measure vegetation cover in terms of PAR and LAI in plant and forest canopies. These devices consist of a handheld 'wand' equipped with sensors for inserting under or into the canopy and an external PAR sensor, *e.g.* Decagon's AccuPar Model LP-80. The Tenmars lux meter by contrast measures visible light (in Lux or Footcandles) and while such measures of photometric light are not relevant to plant growth or survival as PAR and LAI are (Jennings *et al.*, 1999), measuring photometric brightness is capable of making a simple direct measure of light and shade created by vegetation. In addition, the lux meter has the advantage of portability over a ceptometer.[10]

3.11.3. Botanical diversity

3.11.3.i. Woody diversity and botanical diversity at ground level

The woody diversity was evaluated by recording the species of shrub/tree present at each of the 8 sampling points used in the 30m survey section of each hedge. Unfamiliar shrub and tree species, such as Spindle (*Euonymus europaeus*) were identified with

[10] A ceptometer had been borrowed from Frontier, the agronomists advising on the management of University of Lincoln farmland, but the equipment, including handheld device and external sensor, proved too heavy and unwieldy to carry very far in the field by a lone investigator, given the need to carry other equipment and the accessibility on foot only of some hedgerows.

reference to photographic plates in Sterry (2006), but the quality of these photographs was variable and so Sutton (1990) and Rose (2006) were also consulted.

Botanical diversity at ground level was sampled using 2 quadrats per hedgerow measuring 2m x 1m. The quadrats were positioned at points 10m and 20m along the 30m hedgerow survey length, with the 2m axis running down the line of the hedgerow and the 1m axis extending out from the hedgerow bottom (Figs. 3.12 and 3.13). This procedure follows the Hedgerow Survey Handbook (Defra, 2007) guidance.

Measurement of botanical diversity at ground level using quadrats was conducted once in July. This fitted with the recommendation by Hill *et al.* (2005) that vegetation surveys should be conducted at a time of year when the majority of taxa are likely to be visible above ground, large enough for identification and before any major disturbance of the site (*e.g.* harvesting or margin cutting). Diversity of vegetation in the hedge bottom was recorded at the Family level (plus the Division Bryophyta, mosses) as a count of the number of taxa. Where flora could not be identified in the field, photographs were taken for subsequent identification. Flora were identified with reference to Dickinson (2003), Rose (2006) and Sterry (2006).

3.11.3.ii. Botanical diversity at trap position

The botanical diversity of vegetation immediately surrounding the traps at ground level was recorded each month at each of the 8 sampling points/trap positions in each hedgerow. Botanical families within a 25cm radius of the traps were recorded. This was done in order to obtain a more precise view of the localised vegetation conditions in the vicinity of the traps which might be affecting invertebrate activity-density.

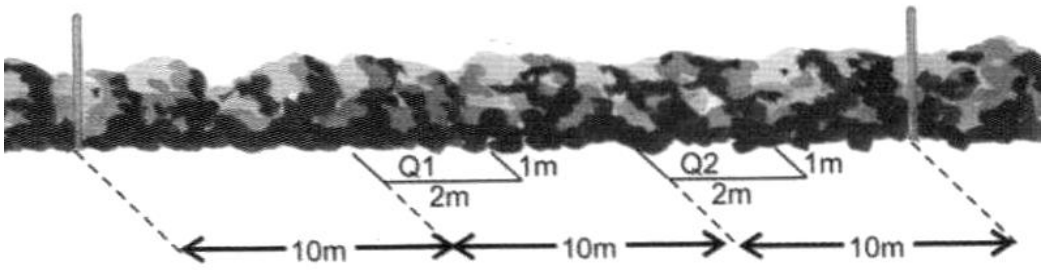


Figure 3.12. Locating the botanical survey quadrats within the survey transects at ground level following the Hedgerow Survey Handbook method. Source: Defra, 2007. © Crown Copyright 2007

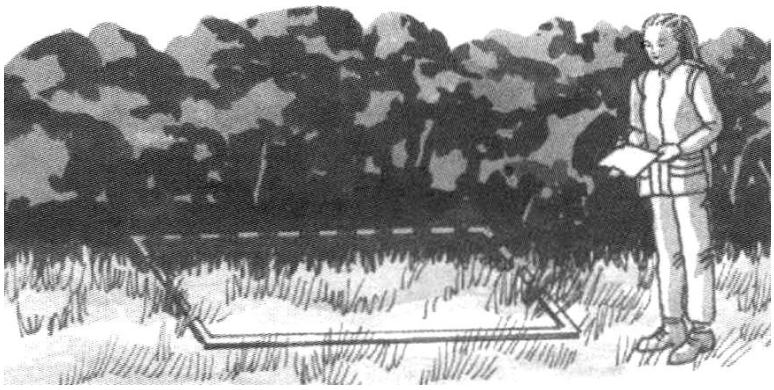


Figure 3.13. Position of ground flora survey quadrats (2m x 1m) in the hedge. Reproduced from the Hedgerow Survey Handbook. Source: Defra, 2007. © Crown Copyright 2007

3.11.4. Weather

Data for temperature, humidity, rain and wind were recorded. Data were taken from the Weather Underground website rather than the Met Office since the latter now gives limited data for free. For the sticky traps, a 4-day average was calculated to cover the duration of the trapping sessions. For the beatings, a 'snapshot' measurement of weather was taken using a Silva ADC Summit handheld digital weather station at the time of sampling from the hedge canopies. Data on temperature, humidity and wind speed were recorded from a single measure immediately prior to conducting beating. A measure of rainfall was not required, since beating was not conducted under rainy conditions.

3.12. Statistical Methods - overview

A range of statistical tests were required to analyse the range of data generated by the hedgerow surveys, from testing for normality to modelling explanatory variables using multivariate techniques. Statistical methods were selected partly based on prior knowledge and readings of relevant texts (*e.g.* Hammer, no date; Fowler *et al.*, 1998; Grafen & Hails, 2002; Sutherland, 2006; Field, 2009; Hawkins, 2009; Zuur *et al.*, 2007; Dytham, 2011; Legendre & Legendre, 2012) and peer-reviewed papers on invertebrates, agro-ecology and hedgerows, *e.g.* Maudsley *et al.* (2002)[11], Pywell *et al.* (2005)[12], Pollard & Holland (2006)[13], Biaggini *et al.* (2007)[14], plus more generally papers discussing statistical methods

[11] Canonical Correspondence Analysis (CCA) used to test relationships between habitat variables and the diversity and abundance of predatory arthropods in a hedgerow

[12]Canonical Correspondence Analysis (CCA) used to test the relationship between hedgerow habitat variables and the presence of overwintering arthropods

[13] Redundancy Analysis (RDA) used to establish whether sampling point within a hedge influenced invertebrate assemblage composition

(*e.g.* Bolker *et al*., 2008 on Generalised Linear Mixed Models and their use in ecology). The advice of a combination of supervisors and other academic staff within the University of Lincoln's School of Life Sciences was also invaluable.

There are multiple possibilities for testing the distribution of data, including both graphical and numerical tests. Histograms of distribution data and the Q-Q plots were generated in SPSS to establish whether data fitted the normal Gaussian distribution pattern, but ultimately reliance was placed on statistical testing in determining whether the data were normally distributed. There are a multitude of normality tests – Razali & Wah (2011) cite circa 40 - but of these SPSS provides two: Kolmogorov-Smirnov and Shapiro-Wilk. Normality of data was tested within SPSS using the Shapiro-Wilk test in preference to the alternative Kolmogorov-Smirnov because Shapiro-Wilk is reckoned to have more power (Razali & Wah, 2011) and is considered to be more appropriate for small sample sizes (< 50 samples), but can also handle sample sizes as large as 2000 (Laerd Statistics, no date).

Gotelli & Ellison (2004) assert that: "normal (bell-shaped) distributions are ubiquitous and turn up frequently in the real world", but other commentators are more circumspect with regard to ecological data and their ability to conform to normal distributions. Anderson (2001), for example, declares that any assumption of a normal distribution is "particularly unrealistic for most ecological datasets" and this is because abundance distributions of taxa are generally highly aggregated or skewed, and datasets may contain lots of zero values for rare taxa. Normality testing using Shapiro-Wilk showed that data were not normally distributed and this could not be 'fixed' (*i.e.* normalised) by transforming the data.

Patterns in all data, including abundance, diversity and explanatory variables, were tested for normality. When non-normal distributions were found in the data, tests tolerant of non-normal data were used, principally the Generalised Linear Model (GLM), and in addition, distribution-free or ranked tests where appropriate (*e.g.* for correlations Spearman's rather than Pearson's).

GLMs are appealing by virtue of providing a unified approach to common statistical procedures and are applied in a range of disciplines including ecology, where they are widely used (Bolker *et al*, 2008). Searching only Agricultural and Biological Science peer-reviewed journal titles in the online database ScienceDirect®[15], for papers

[14]Multidimensional Scaling (MDS) used to test for similarity patterns between invertebrate assemblages of cultivated plots and semi-natural habitats

[15]A database owned by Elsevier B.V.

containing “generalised linear model(s)” or “generalized linear model(s)” anywhere in text, showed that the term was used increasingly over the 10-year period from 2003 to year end 2012, with articles citing the term rising steadily from 188 in 2003 up to 587 by the year end 2012.

Regarding the use of non-parametric statistics to deal with data which deviates from normal distribution, it is acknowledged that such tests are potentially wasteful of information and that parametric analyses are often robust to violations of assumptions of normality (*e.g.* Gotelli and Ellison, 2004). Use of non-parametric tests, such as Kruskal-Wallis, Mann-Whitney *U* and Spearman’s *rho* correlations, has its place in the analysis and is unavoidable in reporting of non-normal data: examples of the use of non-parametric tests in a wide array of published studies on ecological and animal science themes can easily be found (*e.g.* Biaggini *et al.*, 2007; Debras *et al*., 2008; Ruxton & Beauchamp, 2008; Kardol *et al*., 2009; Trigal-Dominguez *et al,* 2010; Shelef & Groner, 2011; Baini *et al.*, 2012; Henriques *et al.,* 2013).

3.12.1. Taxonomic Abundance Distributions

It is recommended that the first thing an investigator should do with abundance data is to plot it as a rank/abundance chart (Magurran, 2004). Conventionally, these charts are called Species Abundance Distributions or SADs, but in this study the name used has been altered to reflect the broader level of analysis, *i.e.* Taxonomic Abundance Distribution. Taxonomic Abundance Distributions (TADs) were calculated and presented based on techniques to calculate Species Abundance Distributions (SAD) outlined in McGill *et al.* (2007) and Magurran and McGill (2011). The TAD enables an immediate (visual) comparison between two different communities and showing for instance which community has the higher proportion of rare species which may be important in making conservation decisions (McGill *et al.,* 2007). A SAD is a description of the abundance of each species encountered within a community, which can be plotted in a number of ways but a rank abundance plot on a simple line chart, of higher level taxa rather than species, is the method chosen for presentation in Chapters 4 and 5, whereby invertebrate abundance is plotted on the y-axis against taxon rank on the x-axis. ‘Taxon ranking’ merely means that individual invertebrate taxa have been ordered according to abundance from the highest to lowest. These ranked taxa appear only as numbers and are not labelled with their taxon identity as is the convention in SADs.

The distributions, found to deviate from a normal distribution, were compared using a rank analysis of covariance (ANCOVA). A rank ANCOVA is a non-parametric version of ANCOVA, which can be calculated by various methods (see Lawson, 1983), but for which the simple Quade (1967) version of the procedure has been used. A description of how the rank analysis is performed can be found on the IBM (no date) website. There is no explicit option for a non-parametric ANCOVA, but one can be produced by: a) converting dependent variables and their covariates into ranks, b) running a linear regression of the ranks of the dependent variable on the ranks of the covariates, saving the unstandardised residuals, and finally c) running an ANOVA, using the residuals from the regression as the dependent variable, and the grouping variable as the factor.

3.12.2. Generalised Linear Model (GLM)

The fundamental count data were identified as having a negative binomial distribution (Fowler *et al.*, 1998). Southwood & Henderson (2000) comment that the distribution of 'most species' can be fitted to a negative binomial and, being a probability model, is to be preferred over other measures of distribution. Sileshi (2008) also commends the use of the negative binomial-linked models because of the "excess zero problem" posed by invertebrate count data. Negative binomial log-linked Generalised Linear Model (GLM) tests were therefore conducted on the abundance data to test whether apparent differences between boundary types and numbers of invertebrates could be supported by statistical evidence. Effects of boundary type and month and their interactions on faunal abundance were tested on each individual taxon. Where no significant interaction was found, the interaction was removed and tests were repeated for main effects only.

A GLM (Tweedie with log link) was also conducted to test the effects of month and boundary type on the various measures of diversity. The Tweedie log link model was chosen based on experimentation with the modelling: it was the only fit that did not produce errors. The Tweedie distribution is appropriate for variables that have a "mixed" distribution in the sense that it combines properties of continuous (takes non-negative real values) and discrete distributions. The dependent variable must be numeric, with data values greater than or equal to zero (SPSS Inc., no date). The Tweedie model reflects the fact that diversity indices are measurement scales based on count data and therefore represent a mixture of continuous and discrete distributions.

3.12.3. Correlations

Non-parametric Spearman's ranked correlations were used to test the relationship between numbers of different taxa. Spearman's correlations were also used to test the relationship between age of hedgerow and abundance of invertebrates. The Spearman coefficient was interpreted to indicate strength of association between paired data based on the following scale (Weir, no date):

- 0.00 – 0.19 = "very weak"
- 0.20 – 0.39 = "weak"
- 0.40 – 0.59 = "moderate"
- 0.60 – 0.79 = "strong"
- 0.80 – 1.00 = "very strong"

Large numbers of correlation tests were conducted so a correction was applied to the significance level to control for false discovery of significant outcomes. Use of Benjamini-Yekuelti FDR (otherwise abbreviated to B-Y FDR) correction on significance levels for multiple comparisons was influenced by reading on alternatives to Bonferroni (notably Narum, 2006). Bonferroni corrections are commonly cited in the literature (*e.g.* Wheater and Cook, 2000), however, they can result in very conservative tests, quickly approaching values close to zero where large numbers of multiple comparisons are made. While trying to prevent Type I errors (rejecting the null hypothesis of no significant difference when in fact it is true), the correction can run the risk of increasing Type II errors (accepting a null hypothesis when it is false). Narum (2006) suggests that the B-Y FDR method has the effect of reducing the risk of making Type II errors by decreasing the rate at which alpha reaches zero, while maintaining a moderately conservative approach to controlling for Type I errors.

Bonferroni is calculated by dividing the alpha level (α) of 0.05 by the number of comparisons made, *e.g.* in the case of 15 tests, the Bonferroni correction would be: 0.05/20 = 0.003. By contrast, a B-Y FDR would be calculated by dividing the alpha level (0.05) by the sum of 1/1, 1/2, 1/3, 1/4, 1/5, 1/6 and so on up to 1/15, such that 0.05/3.319 = 0.015. The formula for B-Y FDR is:

$$\alpha / \sum_{i=1}^{k} (1/i)$$

where k = number of hypothesis tests and i = the number of the test in sequence.

3.12.4. Discriminant/Decision Tree Analysis

In addition to correlations, a type of non-parametric discriminant or decision tree analysis was conducted on invertebrate catches, using Sipina software (Rakotomalala, no date) and an Improved ChAID Tschuprow Goodness of Split (Rakotomalala, 2005). This was to explore the possibilities of being able to distinguish between Mature and New hedges based on the abundance of a particular taxon or combination of taxa at ground level in the hedge bottom. Such analysis generates functions from a sample of cases for which group membership is known and the functions thus generated can be applied to new cases where group membership is unknown. In theory, this would mean that even if we did not know whether the hedge was Mature or New, we could look at the abundances of certain taxa from the hedge bottom and assign the hedges to one or the other age grouping.

3.12.5. Taxon Accumulation Curves

Taxon Accumulation Curves (TACs), showing the accretion or cumulative increase in number of taxonomic groups with increased sampling, were used to test sampling adequacy and based on Species Accumulation Curves (Magurran, 2004). They are also capable of enabling comparisons between the taxon richness of two or more communities. For data collected from hedges only, a comparison was made between the shape of the curves generated for each type of hedge (Mature versus New) at both ground and canopy level. ANCOVA (Quade procedure – see 3.12.1) tests were used to investigate differences between the TACs.

3.12.6. Multivariate statistics

Tests of the effects of explanatory variables on the abundance and diversity of invertebrates collected from the hedgerows were made using a model selection process based on Akaike's information criterion. Akaike (1973; 1974) is regarded as being one of the first to lay the foundation of modern statistical modelling, model identification and evaluation: Bozdogan (1987) called his method simple, versatile, logical, with "enormous practical importance". The technique was widely accepted in some areas of statistics (*e.g.* engineering and psychometrics) from its inception in the early-1970s, but not so popular or well-understood in others. Ecology falls into this the latter area.

Unlike Canonical Correspondence Analysis (CCA) (ter Braak, 1986; 1987), the technique based on the Akaike Information Criterion (AIC and AICc) was not developed for ecology specifically, but from information theory. Nonetheless, it is increasingly being used in analyses in the field of ecology to compare multiple models of explanatory factors

at once (Symonds & Moussalli, 2011). Its growing usage can be illustrated by comparing the number of peer-reviewed journal items citing the Akaike information criterion in the last 15 years: a search of ScienceDirect® shows that the number of items in Agricultural and Biological Sciences journals making reference to the modelling technique has risen dramatically from 40 in 2000 to 1,385 in 2015; whereas Canonical Correspondence Analysis (ter Braak, 1986; 1987) and Redundancy Analysis (Wollenberg, 1977), which are also related to multiple linear regression and widely used in detecting relationships between taxonomic composition and environmental variables (Legendre & Legendre, 2012), have seen a six-fold and five-fold increase respectively. This increasing popularity of AIC suggests a widespread usefulness.

The method is exploratory and enables comparison and ranking of multiple competing explanatory models and estimate which of them best approximates processes underlying the biological phenomenon being studied (Symonds & Moussalli, 2011). It enables the identification of optimal, parsimonious models from competing models: AIC values are in themselves meaningless as a stand-alone value and derive meaning from comparison with the AIC values of other models, with the model having the lowest AIC value representing the best approximation of an explanatory model. It is therefore a method of handling explanatory variables which acknowledges the difficulty of providing an absolute truth when explaining complex ecological patterns. Symonds & Moussalli (2011) have produced something of a novice's guide to the use of Akaike's information criterion in model selection. Kervinen *et al.* (2012) demonstrated how AIC modelling can assist in determining the best explanatory models.

The AIC modelling was performed using the statistical free software R (www.r-project.org), and model ranking was performed in excel using AIC values generated by generalised linear models. The analysis looked at main effects only, no interaction terms were used. The results of Akaike information criterion analysis of my data are presented in Chapter 6, which compares the 'fit' of factors relating to botanical diversity, hedgerow structure, and weather with invertebrate abundance and diversity in the hedge bottom and hedge top or 'canopy'.

Chapter 4. Effects of hedge age on invertebrate assemblages at ground level

4.1. Introduction

It was not until government-funded environmental programmes, so-called agri-environmental schemes (AES), were introduced in the 1980s, that there were systematic attempts to restore a much-degraded farmland hedgerow network with new planting and improved management (Staley *et al.*, 2012a). Agri-environmental schemes in one form or another have been in place since 1987 in the UK, with one of their principal aims being the conservation and enhancement of farmland biodiversity (Grice *et al.*, 2007). The Countryside Stewardship Scheme (CSS) was introduced in 1991, originally as a pilot and then as a fully-blown scheme, to encourage farmers to improve the environmental management of their farmland. Environmental Stewardship replaced Countryside Stewardship in 2005, with more specific goals, including a primary objective of conserving wildlife and biodiversity through habitat creation, restoration and appropriate management. As an important part of our farmed landscape, "the most widespread semi-natural habitat in England" (Hedgelink, 2009), hedgerows have figured prominently in agri-environment schemes. The Countryside Stewardship Scheme promoted widespread hedge-planting and funding for hedgerow planting continues, albeit to a more limited degree, under Higher Level Stewardship (Natural England, 2012 a, b, c). Subsidies are now targeted more towards management rather than planting of new hedgerows (*e.g.* Staley *et al*., 2012b; 2013), but the question remains as to what has been achieved by liberal addition of thousands of hedgerow kilometres to the landscape. The young products of agri-environmental planting activity are a frequent sight in the farmed landscape, interspersed with the pre-existing mature hedgerows, from previous decades and centuries. But what are they contributing in terms of the conservation if not enhancement of biodiversity? In the case of invertebrates, how can we determine any enhancements at the level of both abundance and diversity?

In the past two decades or so a substantial amount of research activity has been undertaken in support of AES, to refine practical advice to farmers to improve biodiversity gains, and increasingly to monitor the results of putting different options in place (Boatman *et al.*, 2010). Research has shown variable results for hedgerow options, with some studies reporting wildlife benefits (*e.g.* Hof & Bright, 2010) and others suggesting that

farmland hedgerows may not be delivering the anticipated returns (*e.g.* Bates & Harris, 2009). There are a few studies that provide any assessment of the value of AES to hedgerow invertebrates and these tend to focus their efforts on the 'usual suspects', *i.e.* Coleoptera (especially Carabids and Staphylinids) and Araneae, while acknowledging that there is a deficit of information on how the broad range of invertebrate taxa are affected by hedgerow creation/restoration (Griffiths *et al*., 2007). Deeming *et al.* (2010) made a contribution to plugging this gap via a small-scale single farm study of the invertebrate assemblages of hedgerows planted under environmental stewardship and their more mature counterparts established prior to environmental programmes. The study concluded that mature hedgerows (≥50 years) had greater invertebrate diversity than newly planted hedgerows (≤5 yrs) and the invertebrates of new hedges were consistently more abundant than in mature hedges. The study was limited to a small number of hedgerows and the intention with the current study was to extend previous work investigating whether the effect of the presence of a new hedgerow on the abundance and diversity of invertebrates held true on a larger scale, over multiple farming locations.

This study makes a comparison of young (~6 to 15 years, planted under AES) and mature (>50 years) hedgerows in terms of their invertebrate abundance and diversity and examines whether any effects of new habitat creation and/or 'maturity' can be detected. Maturity is used here as a relative term, given the fact that the hedgerow landscape is in its origins many centuries old (Dowdeswell, 1987). The mature hedgerow habitats were assumed to represent a more advanced stage of use/colonisation and thus anticipated to show superior invertebrate diversity. Means of representing this diversity were also explored.

As illustrated in the General Methodology, integral to the structure of the hedgerow habitat is the more or less grassy margin or 'verge' at the hedge bottom (Dowdeswell, 1987; Maudsley, 2000; New, 2005a). Therefore any assessment of hedgerow invertebrate abundance and diversity should include sampling of the invertebrates of the 'verge' as well as the woody body of the hedgerow. This chapter focuses on the fauna of the hedge bottom and examines the effects of boundary type (young, mature or no hedgerow) on invertebrate assemblages as a whole rather than focusing specifically on pest or beneficial species or on any single 'indicator' or 'surrogate' taxon.

As discussed in the General Methodology, indicator taxa such as butterflies, Carabid or Staphylinid beetles and spiders, have been commonly used as 'surrogates' for total arthropod/insect diversity in evaluations of the quality of semi-natural habitats (*e.g.*

Büchs, 2003b; Barr *et al.*, 2005; Thomas, 2005; Biaggini *et al*., 2007; Griffiths *et al.*, 2007; Brooks *et al.*, 2012; Defra/JNCC, 2013*)*. The idea of using a taxonomic group as an indicator to effectively represent total diversity is however controversial, with some investigators insisting there is no best correlating arthropod group indicating biodiversity in agricultural environments (Duelli, 1997; Duelli & Obrist, 1998; Duelli *et al.*, 1999). Family-level (and genus-level) diversities are considered by some to be very good indicators of underlying species diversities in ecology and palaeontology (*e.g.* Lee, 1997; Gaston, 2000), although certain research in agro-ecosystems suggests otherwise (*e.g.* Biaggini *et al*., 2007). Duelli & Obrist (1998, 2003) and Duelli *et al*. (1999) recommended an "optimal approach", whereby a "basket" of indicator taxa are used, suggesting aculeate Hymenoptera (bees, wasps and ants), Hemiptera and Syrphidae (hoverflies). Duelli & Obrist (2003) observed that there were few published examples of the correlation between a group or several groups of species.

Researchers are still pursuing the 'holy grail' of suitable biodiversity indicator groups (Gerlach *et al*., 2013): Anderson *et al.* (2011), for instance, have proposed the use of a count of numbers of parasitic Hymenoptera, rather than the very difficult task of identification of this group, for monitoring biodiversity in agro-ecosystems. In a previous study of hedge bottom invertebrates by Deeming *et al*. (2010), discriminant analysis identified a 'basket' of six Orders which accounted for the main difference between the hedge types: Hymenoptera, Collembola, Opiliones, Mecoptera, Araneae and Julida.

My investigation was based on a view of the whole assemblage, under the premise that the invertebrate fauna of relatively well-established mature hedgerows was likely to exhibit a more diverse assemblage than that of less well-established newly-planted hedgerows, and that invertebrates were likely to be less diverse in the grassy hedgeless boundaries (Pywell *et al.*, 2005; Deeming *et al*., 2010; Ernoult *et al.* 2012). Pywell *et al.* (2005) studied the results of boundary creation under AES and found that there was no effect of boundary habitat maturity on the abundance or diversity of overwintering Coleoptera or Araneae. At the time this study was proposed (2010), the author knew of no other more recent similar published studies which looked beyond Coleoptera and Araneae to examine the response of a broader range of invertebrate taxa to hedgerow planting under AES. This still seems to be the case, although Amy *et al.* (2015) have examined the effects of rejuvenation techniques, notably laying, on a range of invertebrate groups.

The present study represents an extension of previous work investigating the effect of age of hedgerow on the abundance and diversity of ground-occurring invertebrates of

new (~3 year-old) and mature hedgerows, which was based on a much smaller sample size of boundaries (Deeming *et al.*, 2010). This previous work indicated that mature hedge bottoms were consistently more diverse than new hedges over a 1-year period. Diversity was measured by a count of Orders/Classes and their respective abundances following a method suggested by Biaggini *et al.* (2007) as being suited to at least initial invertebrate biodiversity assessment in the farmed environment. The inclusion in this investigation of more boundaries and the addition of a selection of hedgeless boundaries for comparison enables a more robust interpretation of how the presence of hedgerows affects invertebrate biodiversity.

Previous work employed pitfall traps (Deeming *et al.*, 2010) and indeed pitfall trapping is commonplace in studies of ground-active invertebrates of agricultural environments (New, 1998), including hedgerows and field margins (*e.g.* Gruttke & Kornacker, 1994; Fournier & Loreau, 1999; Holland *et al.*, 2001; Asteraki *et al.*, 2004; Pywell *et al.*, 2005; Griffiths *et al.*, 2007; Hof & Bright, 2010; Pywell *et al*., 2011; Hof *et al*., 2012). On this occasion sampling was conducted using sticky traps and thus the study represents in part an experimental use of an alternative trapping method, which catches a different assemblage from pitfall traps (pilot work in Chapter 3 and Appendix A).

I investigate the basic hypothesis that hedge maturity is a key factor in composition of invertebrate assemblages. I evaluate enhancements in invertebrate abundance and diversity achieved by agri-environmental hedgerow planting. In so doing, I examine whether a biodiversity assessment using broad taxonomic groups, as suggested by Biaggini *et al.* (2007), and whether other 'simplified' or surrogate measures such as family diversity, or sheer abundance of certain groups, such as indicated by Deeming *et al.* (2010) and Anderson *et al.* (2011), allows us to discriminate between (h)edge types and thereby gauge the biodiversity gains of newly-planted hedges.

This Chapter examines the abundance and diversity of the invertebrate fauna of the hedge bottoms only. Chapter 5 examines the effects of hedgerow maturity on 'canopy-active' invertebrate fauna present in the woody element of the hedgerow using a beating technique. Other explanatory factors, complementary to or interacting with effects of maturity, will be discussed in Chapters 6 and 7.

4.2. Methods

Ground-occurring invertebrate taxa were surveyed using sticky traps as described in Chapter 3 and Appendix 3, but briefly sticky trapping took place at the four farm sites on 3 separate occasions during April, July and September 2011. The 36 hedgerows/field boundaries (Mature hedges (n = 16), New hedges (n = 16), Hedgeless boundaries (n = 4) were visited in groups of 6 on successive days, never in the same order. Eight traps were placed equidistant at 4 m apart in the hedge bottom/hedgeless grassy boundaries along the central 30m section of the selected boundaries. The traps were placed at hedge bottom within an area of the margin up to 1.5m from the centre line of the hedgerow, falling within the 2m cross-compliance 'protection zone'. In the case of the hedgeless boundaries, traps were set within 1.5m of a notional centre line. Traps were left active for 96 hours (4 days). A total of 864 traps were used (288 per month). Traps were covered with a wire mesh cage to deter vertebrate predators and prevent by-catch of vertebrate taxa.

After collection, sticky traps in their demi-diamond holders were removed from the wire mesh cages and placed in a domestic freezer and were stored until analysis. Invertebrates were examined using a binocular zoom dissecting microscope (up to x90 magnification) and identified down to major taxonomic group Order/Class using Tilling (1987) principally for guidance, but with reference to other texts, including Alford, 1999; 2011; Gibb & Oseto, 2006; Chinery, 2007). Tilling (1987) defines Collembola as an Order, but they are currently considered as a Class (Hopkin, 2007). Species-level identification of all specimens was not an achievable aim of this study, nonetheless classifications below the level of Order, were made for the three most speciose groups – Hymenoptera, Coleoptera and Diptera. Following invertebrate identification the sticky trap pads were removed from the demi-diamond holders and stored dry in slotted boxes at ambient temperature.

Along with data on invertebrate abundance and diversity, a range of variables relating to the structure and composition of the hedgerows (dimensions, margin sward, botanical diversity, vegetation density) and weather conditions were recorded. These variables and methods of collecting them are described in the General Methodology and their effects are examined separately in Chapter 7.

Data were organised, processed and presented graphically using Microsoft Excel 2007 and statistical analysis was performed using IBM SPSS Statistics for Windows, Version 19.0 (Released 2010). Since the data were not normally distributed, statistical tests tolerant of non-normal data were employed.

The structure of the invertebrate assemblages was measured in a number of different ways, using methods of visualisation, *i.e.* ranked abundance distributions, aka Whittaker plots, (Magurran, 2004; Magurran & McGill, 2011) and taxon accretion curves. Ranked ANCOVA (Quade, 1967) was used to analyse differences between the ranked abundance distributions and also subsequently between the taxonomic accretion curves of the different habitats. In addition, the diversity of the assemblages was explored, using a selection of measures/indices that highlighted different aspects of assemblage structure such as richness, evenness, dominance and heterogeneity (as described and recommended by Magurran, 2004).

The principal means of testing for differences in abundance and diversity of invertebrates between habitat types and months was through a Generalised Linear Model (GLM; Nelder and Wedderburn, 1972). Both interactions and main effects (where no significant interaction could be found) were tested.

Tests for correlations between age and taxon abundance and diversity were conducted using Spearman's *rho* rank correlations with a B-Y method FDR correction (Benjamini & Yekutieli, 2001, as described by Narum, 2006). In addition, multiple Spearman's *rho* correlations (using the B-Y FDR correction method) were performed to investigate whether any individual taxon was sufficiently well-correlated with other taxa to act as a surrogate for the overall abundance and diversity of the invertebrate assemblage.

A type of discriminant analysis was conducted on the invertebrate count data to help determine whether the abundance of any group of taxa could be used to differentiate between hedge types (as indicated by Deeming *et al*., 2010), and therefore be capable of acting as indicators or surrogates for overall diversity. Stepwise discriminant analyses are parametric tests (IBM, 2010) which can be employed to evaluate such differences, but for count data which deviate from normality, alternative techniques should be employed. Alternatives to parametric tests include data mining techniques such as ID3 (Quinlan, 1986) and ChAID (Kass, 1980) which conduct decision tree analysis on data in order to predict classification into clearly discriminated groupings. Here, an adaptation of ChAID decision tree analysis, Improved ChAID Tuprow Goodness of Fit analysis (Rakotomalala, 2005) was used.

Main results are reported in section 4.3 and supporting data is provided in Appendix B where indicated. Correlations, for instance, returned numerous non-significant pairwise comparisons and these are not included in the results section itself, but summarised in the text, and presented in full in Appendix B for completeness.

4.3. Results

4.3.1. Abundance of invertebrates at ground level/hedge bottom and their taxonomic groups – overview

A total of 64,255 invertebrates from 22 taxonomic groups were collected at ground level from the hedges and boundaries during April, July and September 2011 (Table 4.1). Although a total of 22 major taxonomic groups (Classes/Orders) were found in the boundaries, there was no single boundary or boundary type in which all 22 groups were collected. Taxonomic abundance ranged from thousands of individuals, to the very 'rare', or infrequently sampled, numbering only one ('singleton') or two ('doubleton').

A marginally higher number of groups were found in Mature hedges (20) than in New hedges (19) or Hedgeless boundaries (17) in total. Hedgeless boundaries had the overall highest frequency of 'rare' and/or infrequently sampled taxa, but from a smaller number of samples (Appendix B, Table B1). Incidence of 'rare' taxa was similar in Mature and New hedge types. Although fewer Hedgeless boundaries were sampled, yielding lower invertebrate abundance than Mature and New hedges, mean counts did exceed those of both Mature and New hedges for Araneae and Hemiptera. In Hedgeless boundaries for Geophilomorpha, Mecoptera, Neuroptera, Polydesmida and Psocoptera there were no recorded specimens in any month. By comparison, no occurrences of Geophilomorpha, Neuroptera or Pseudoscorpiones were recorded in New hedges, and in Mature hedges no individuals were recorded for Mecoptera or Orthoptera.

Plots of the general distribution of organisms for each hedge/boundary type and month are shown in Figures 4.1a-c, in which the abundance of individuals has been plotted against taxonomic rank to produce ranked Taxonomic Abundance Distributions (TADs), based on Species Abundance Distributions (SADs) or so-called Whittaker plots. In keeping with the classic shape of a SAD/Whittaker plot, these plots show, for April and July at least, an approximation of the universal "hollow curve" (Magurran, 2004). This is a long-recognised, not unexpected, ecological pattern, reflective of low evenness across the diversity of biota, which indicates a few abundant fauna, other moderately common taxa and a remainder of species, "often the majority" (Magurran, 2004), present at a low level. Although the data do show some small fluctuations, the fundamental shape is maintained in the Spring and Summer months for all boundary types. In September, the plot takes on a shallower shape with less separation between the boundary types, indicating a more even distribution of less frequently-occurring taxa.

A ranked ANCOVA (Quade procedure) indicated a statistically significant difference between the TADs of boundary types in April and July but not in September, when differences between assemblages seem dampened down and this is reflected in the appearance of a gentler slope rather than a curve *per se* (Table 4.2). In July there are statistically significant differences between the structures of the assemblages of the two hedge types and the hedge-free boundaries. In April, post hoc multiple comparisons indicate that the key difference lies between Mature hedges and Hedgeless boundaries, whilst in July the significant differences are between Mature hedges and Hedgeless boundaries, and also between New hedges and Hedgeless boundaries. In September there are no significant differences between habitat types in their abundance distributions. As the TAD charts do not identify what influences these shapes, further analysis of taxonomic groups in relation to hedge/boundary type and month follows.

Table 4.1. Taxonomic rank showing total abundance of invertebrates for individual taxa ranked from most to least abundant. Totals for each month (April, July, September) and a grand total for All months and All boundaries (Mature hedges, New hedges and Hedgeless boundaries combined) are shown. Invertebrates collected from sticky traps at ground level

	Total abundance, all boundaries summed							
	All months (n = 107)		April (n = 36)		July (n = 36)		September (n = 35)	
Rank	Taxon	Total	Taxon	Total	Taxon	Total	Taxon	Total
1	Collembola	16,386	Collembola	9,449	Hymenoptera	7,971	Hymenoptera	2,162
2	Hymenoptera	12,939	Acari	2,885	Acari	7,619	Diptera	2,041
3	Acari	12,180	Hymenoptera	2,806	Collembola	5,021	Collembola	1,916
4	Hemiptera	5,883	Diptera	1,138	Hemiptera	3,347	Acari	1,676
5	Diptera	4,905	Hemiptera	1,112	Thysanoptera	2,426	Opiliones	1,518
6	Opiliones	3,039	Coleoptera	963	Diptera	1,726	Hemiptera	1,424
7	Thysanoptera	3,012	Araneae	670	Opiliones	1,213	Coleoptera	688
8	Coleoptera	2,826	Thysanoptera	429	Coleoptera	1,175	Araneae	340
9	Araneae	1,708	Opiliones	308	Araneae	698	Isopoda	184
10	Isopoda	519	Dermaptera	60	Dermaptera	315	Thysanoptera	157
11	Dermaptera	388	Isopoda	55	Isopoda	280	Julida	83
12	Lepidoptera	137	Lepidoptera	40	Lepidoptera	73	Psocoptera	46
13	Julida	125	Julida	18	Pulmonata	46	Lepidoptera	24
14	Psocoptera	71	Pulmonata	11	Julida	24	Siphonaptera	18
14	Pulmonata	71	Psocoptera	4	Psocoptera	21	Polydesmida	15
16	Siphonaptera	32	Polydesmida	3	Siphonaptera	14	Pulmonata	14
17	Polydesmida	21	Geophilomorpha	1	Polydesmida	3	Dermaptera	13
18	Pseudoscorpiones	4	Neuroptera	1	Neuroptera	1	Pseudoscorpiones	4
19	Mecoptera	3	Orthoptera	1	Orthoptera	1	Mecoptera	3
20	Orthoptera	3	Siphonaptera	0	Geophilomorpha	0	Orthoptera	1
21	Neuroptera	2	Mecoptera	0	Mecoptera	0	Geophilomorpha	0
22	Geophilomorpha	1	Pseudoscorpiones	0	Pseudoscorpiones	0	Neuroptera	0
	All taxa	64,255	All taxa	19,954	All taxa	31,974	All taxa	12,327

Table 4.2. Results of a ranked ANCOVA (Quade procedure) and LSD post hoc multiple comparisons of taxonomic abundance distributions for each boundary type (Mature hedges, New hedges and Hedgeless boundaries) and month of sampling (April, July and September)

Month	df	F	*p*	Multiple comparisons between boundary types	Mean difference	*p*
April (Fig. 4.1a)	2, 44	4.954	0.011	Mature hedge v. Hedgeless boundary	1.761	0.003
July (Fig. 4.1b)	2, 47	6.052	0.005	Mature hedge v. Hedgeless boundary	2.322	0.001
				New hedge v. Hedgeless boundary	1.545	0.026
Sept (Fig. 4.1c)	2, 50	1.175	0.317	No significant differences	-	-

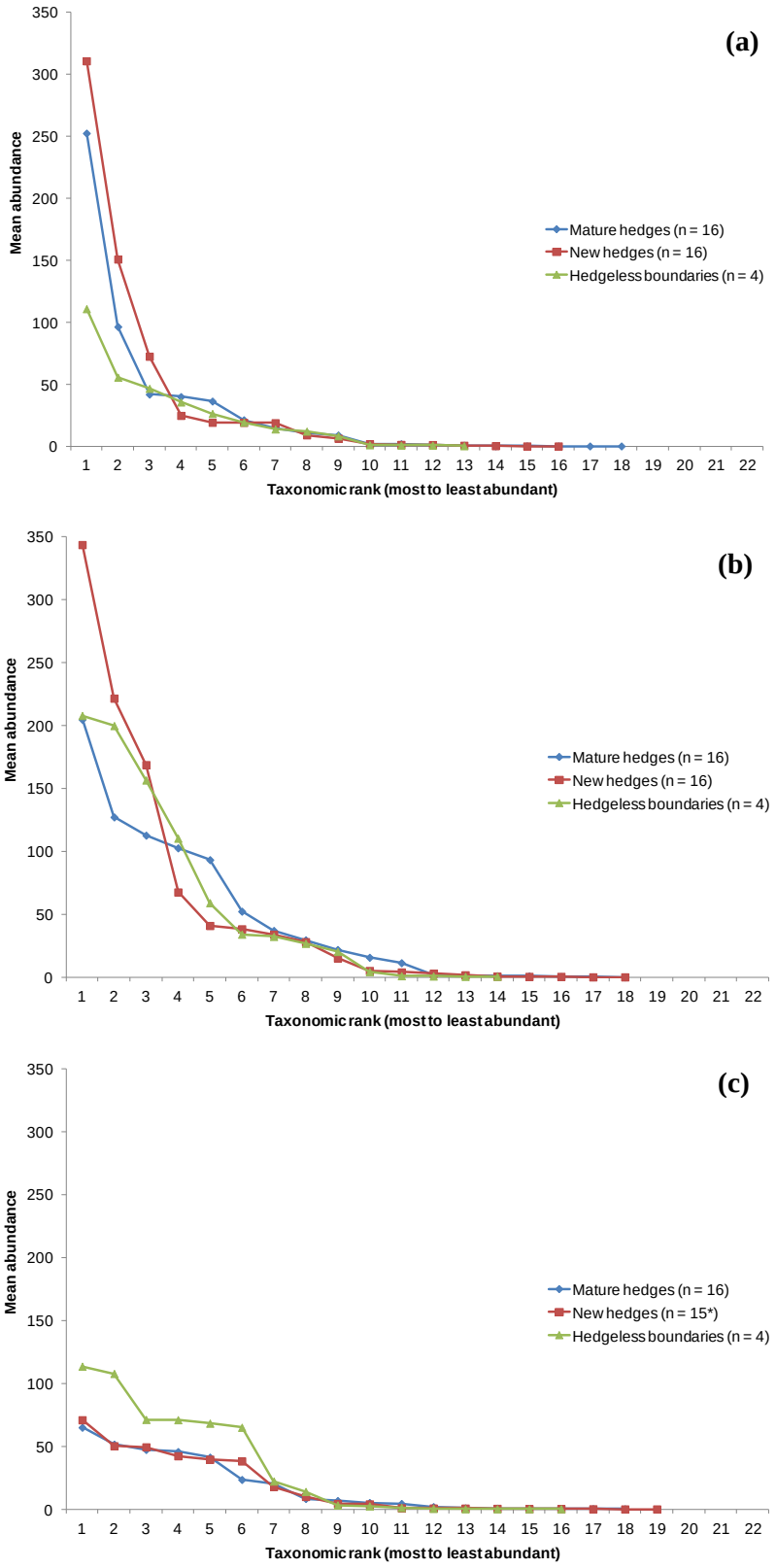
4.3.2. Effect of time of year and boundary type on the abundance of invertebrates at ground level/ hedge bottom

The Generalised Linear Model (GLM) indicated a significant interaction of month and boundary type for Hymenoptera and Dermaptera only (Table 4.3); the nature of these interactions are commented on below (section 4.3.3). Tests for main effects showed a statistically significant effect of boundary type on the abundance of a number of taxa, but a stronger effect of month. A significant effect of hedge age/boundary type was shown for 8 taxa: Araneae, Dermaptera, Hemiptera, Hymenoptera, Isopoda, Julida, Psocoptera and Thysanoptera (Table 4.3). By contrast, the GLM showed a highly significant effect of month on the majority of taxa (14 of the 16 taxa for which analysis was possible). Coleoptera and Siphonaptera[16] showed no significant effect of either month or boundary type.

4.3.3. Abundance of individual invertebrate taxa at ground level/ hedge bottom

The following taxon-by-taxon account describes in greater detail patterns of invertebrate distribution across boundaries and months. In addition to Table 4.1 above, supporting data, showing month-by-month count data (including means, ±SD and ±SE) for each taxon and boundary type, have been tabulated and can be found in Appendix B, Tables B1–B4. There is no consistent seasonal or spatial pattern or trend for all taxa, although for some individual groups abundance data showed a similar shape through the seasons irrespective of hedge/boundary type.

[16] Siphonaptera, although not strictly 'free-living' as adults are included here for completeness as a reflection of the entire fauna collected from sticky traps.



*One New hedgerow removed due to building work

Figure 4.1. Taxonomic Abundance Distribution plots for invertebrates collected from hedge bases in 2011: (a) April; (b) July; (c) September. Line plots show mean number of organisms per hedge/boundary against taxonomic rank (most to least abundant) for all boundary types (Mature hedges, New hedges and Hedgeless boundaries)

Collembola (springtails) were the most abundant taxon overall by some margin (Table 4.1). Mean counts of Collembola showed a similar pattern for both Mature and New hedges across the months, peaking in April and declining through July and September (Fig. 4.2a). By contrast, Hedgeless boundaries showed an apparently 'bell-shaped' pattern, peaking in July, and exhibiting higher abundance than either hedge type in September. New hedges were marked by consistently higher mean abundance of Collembola across the months than Mature hedges. GLM indicated a statistically significant effect of month but no effect of boundary type was observed and the interaction was non-significant (Table 4.3).

Hymenoptera (sawflies, bees, ants and wasps) were the second most abundant taxon overall, and the most abundant taxon in both July and September (Table 4.1). New hedges demonstrated consistently greater abundance of Hymenoptera than Mature hedges or Hedgeless boundaries for all months (Fig. 4.2b). Patterns of mean abundance for Hymenoptera were rather similar in Mature hedges and Hedgeless boundaries, but in New hedges, mean abundance was markedly higher than for the other two boundary types in both April and July, with numbers spiking considerably in July (as indicated by the significant interaction identified by GLM; Table 4.3). New hedges were also marked by a larger amount of variability in values than for either other boundary type, particularly in the peak month, July.

Differences in mean abundance for Hymenoptera were accounted for by comparatively high numbers of Formicidae (ants) present in a few New hedges. In April two New hedges accounted for circa 70% and 20% of Formicidae respectively and just one New hedge accounted for over 90% of Formicidae caught in all New hedges in July (Appendix B, Figs. B1a-c). In September, although the differences between New and Mature hedges and Hedgeless boundaries were less extreme, the numbers of Formicidae did not dominate Hymenopteran fauna quite so strongly as in previous months. The Hymenopteran fauna of Mature hedges were dominated by Parasitic Wasps, accounting for circa 90% of total numbers of Hymenopterans. Hymenopteran fauna of Hedgeless boundaries was also largely accounted for by Parasitica (Appendix B, Figs. B1a-c).

Acari (mites and ticks) were the third most abundant taxon overall (Table 4.1). Mean abundances of Acari showed a remarkably similar pattern for all boundary types across the months (Fig. 4.2c). The GLM indicated a significant effect of month on abundance of Acari, but not of boundary type (Table 4.3).

Table 4.3. Results of a Generalised Linear Model (GLM) analysis of the abundance of all invertebrate taxa collected by sticky trap from the hedge bottom, comparing the effect of time (Month: April, July, September) and habitat (Boundary type: Mature hedges, New hedges and Hedgeless boundaries). Values are Wald χ^2 plus significance values

Taxon	Month		Boundary type		Interaction Month* Boundary type	
	Wald χ^2	*p*	Wald χ^2	*p*	Wald χ^2	*p*
Acari (Fig. 4.2c)	24.880	<0.001	0.378	0.828	2.315	0.678
	39.029	**<0.001**	0.353	0.838	Main effects only	
Araneae (Fig. 4.2i)	7.076	0.029	6.576	0.037	6.929	0.140
	9.193	**0.010**	**7.223**	**0.027**	Main effects only	
Coleoptera (Fig. 4.2h)	2.631	0.268	3.023	0.221	1.415	0.842
	3.974	0.137	3.108	0.211	Main effects only	
Collembola (Fig. 4.2a)	17.587	<0.001	2.109	0.348	6.987	0.137
	44.019	**<0.001**	3.014	0.222	Main effects only	
Dermaptera* (Fig. 4.2k)	**17.693**	**<0.001**	**9.897**	**0.007**	**8.515**	**0.036**
Diptera (Fig. 4.2e)	6.142	0.046	2.600	0.273	0.589	0.964
	6.996	**0.030**	2.643	0..267	Main effects only	
Hemiptera (Fig. 4.2d)	17.719	<0.001	6.903	0.032	9.187	0.057
	22.827	**<0.001**	**7.952**	**0.019**	Main effects only	
Hymenoptera (Fig. 4.2b)**	**29.032**	**<0.001**	**31.781**	**<0.001**	**14.553**	**0.006**
Isopoda (Fig. 4.2j)	18.864	<0.001	8.831	0.012	0.682	0.0.954
	33.279	**<0.001**	**9.448**	**0.009**	Main effects only	
Julida* (Fig. 4.2m)**	2.109	0.348	14.486	0.001	5.605	0.132
	18.399	**<0.001**	**19.855**	**<0.001**	Main effects only	
Lepidoptera (Fig. 4.2l)	3.760	0.153	0.986	0.611	4.310	0.366
	11.093	**0.004**	2.017	0.365	Main effects only	
Opiliones (Fig. 4.2f)	37.565	<0.001	0.911	0.634	2.675	0.614
	48.684	**<0.001**	0.954	0.621	Main effects only	
Psocoptera*(Fig. 4.2n)	17.572	<0.001	3.317	0.069	0.142	0.931
	19.588	**<0.001**	**4.664**	**0.031**	Main effects only	
Pulmonata*(Fig. 4.2o)**	9.404	0.009	2.492	0.288	5.480	0.140
	15.909	**<0.001**	3.109	0.211	Main effects only	
Siphonaptera*(Fig. 4.2p)	0.003	0.958	1.970	0.373	0.915	0.633
	0.352	0.553	2.127	0.345	Main effects only	
Thysanoptera (Fig. 4.2g)	57.340	<0.001	11.161	0.004	5.926	0.205
	104.077	**<0.001**	**11.584**	**0.003**	Main effects only	
Geophilomorpha **Mecoptera** **Neuroptera** **Orthoptera** **Polydesmida** **Pseudoscorpiones**	Validity of model fit uncertain. Too few values to generate results for main effects or interactions.					

*On testing for interaction and main effects, the GLM warned that some convergence criteria not met and validity of model fit uncertain. The Dermaptera dataset contained numerous zero values and they were very rare in the Hedgeless boundaries. Psocoptera present only in hedges and sparse in all months but September. Siphonaptera present in only 2 months and dataset sparse.

**On testing for interaction, the GLM gave warning that maximum number of step-halvings reached but log likelihood value could not be improved. Output for last iteration displayed. Validity of model fit uncertain.

***On testing for interaction, the GLM warned that some convergence criteria not met and validity of model fit uncertain. Julida and Pulmonata datasets contain numerous zero values.

Hedgeless boundaries yielded the highest abundance of Hemiptera (bugs) on average, far exceeding numbers of Hemiptera in both hedge types, in both July and September (Fig. 4.2d). New hedges resembled Hedgeless boundaries across the months, and both differed from Mature hedges, which showed abundance dropping off more markedly in September. Both boundary type and month had a significant effect on abundance (Table 4.3).

Mean numbers of Diptera (true flies) were similar between the three boundary categories, showing very similar patterns of abundance across the months, and peaking in September (Fig. 4.2e). GLM analysis of main effects showed a non-significant effect of boundary type but month had a significant effect on numbers (Table 4.3).

Approximately 90% of the Diptera were identified to superfamily/family, with unidentified specimens due to difficulties with larval forms and partial remains of adults. Sciaridoidea and other generally small and often delicate Nematocera, including fungus gnats (e.g. Cecidomyiidae and Psychodidae), dominated the Dipteran assemblage in April and September. Brachycera, also represented by many smaller to minute taxa, *e.g*. Agromyzidae, Phoridae, Dolichopopidae, were relatively less abundant in those months. In July, Nematocera were greatly outnumbered by Brachycera, in particular Phorids which represented the single largest family of flies for both hedge types and hedgeless boundaries (Appendix B, Tables B5-B7). Generally, Nematocera were relatively more important in Mature hedges and Brachycerans in New hedges and Hedgeless boundaries. Even though Diptera as a group showed no differences between boundaries, when counts were modelled at superfamily/family level, the GLM indicated that there was no significant effect of month but a significant effect of boundary type: Wald $\chi^2 = 9.807$, $p = 0.007$.

Seasonal abundance for Opiliones (harvestmen) was very similar between both hedge age types and Hedgeless boundaries, with numbers peaking in September (Fig. 4.2f). GLM showed a highly significant effect of month but not boundary type, the interaction was non-significant.

Numbers of Thysanoptera (thrips) peaked in July for all boundary types (in the case of Mature hedges a pronounced ‘spike’) with lower abundances for April and September (Fig. 4.2g) with a highly significant effect of month and boundary type (Table 4.3). Thysanoptera was one of a handful of taxa for which mean abundance was consistently higher in Mature hedges than in any other boundary type in every month.

Although numbers of Coleoptera (beetles) were higher in Mature hedges than in New hedges, and Hedgeless boundaries showed the highest mean abundance in September

(Fig. 4.2h) GLM indicated that there was no statistically significant effect of either month or boundary type (Table 4.3). Over 90% of Coleoptera were sorted to superfamily/family level, with unidentified specimens due to larval or partial remains only being present in the sticky traps. Carabids and Staphylinids were prominent throughout the months in all three types of boundary and accounted for very similar portions of the beetle assemblage in July (Appendix B, Tables B8-B10). Carabids formed a particularly important part of the beetle assemblage in Hedgeless boundaries in September. Beetles on the sticky traps tended to consist of smaller members of these families, often <10mm and <5mm for Carabids and Staphylinids respectively. Small (< 3mm) fungivorous beetles, notably Cryptophagidae, Latriididae, Leiodidae and Ptilidae, were well-represented in all boundary types. Curculionids (weevils) were important in New hedges and Hedgeless boundaries in April and July particularly. Elateridae formed a prominent part of the beetle fauna in Hedgeless boundaries in July, but most were found in one boundary. When counts were modelled at superfamily/family level, the GLM indicated that there was no significant effect of month but a significant effect of boundary type: Wald $\chi^2 = 68.930$, $p < 0.001$.

Araneae (spiders) were consistently and markedly more abundant in Hedgeless boundaries than either hedge type (Fig. 4.2i). Mature hedges displayed a more-or-less bell-shaped pattern with a peak in abundance in July. By contrast, New hedges and Hedgeless boundaries showed a peak in abundance in April with a gradual decline thereafter. GLM showed statistically significant effects of both month and boundary type for this taxon, but no interaction (Table 4.3).

Total numbers of Isopoda (woodlice) were in the hundreds rather than the thousands (Table 4.1). The fundamental monthly pattern of abundance was similar for each boundary type, albeit at different scales with a peak in July (Fig. 4.2j). Mature hedges consistently showed the highest abundance for Isopoda across the months. Nearly twice as many Isopoda were found in Mature hedges as New hedges. GLM tests indicated a highly significant effect of month and boundary type but no interaction (Table 4.3).

The majority of Dermaptera (earwigs) were found in Mature hedges with New hedges showing fewer numbers and Hedgeless boundaries showing the lowest abundance of all, including a zero count for April (Fig. 4.2k). Patterns of abundance were broadly similar for Mature and New hedges. In July however the difference between the hedge types was appreciable. GLM showed a statistically highly significant effect of month and a significant effect of boundary type on abundance, as well as a significant interaction (Table 4.3).

Lepidoptera (butterflies and moths) numbered only just in excess of 100 individuals in total for all months and boundaries (Table 4.1) and consisted largely of larval forms and micro-moths, split between approximately 70% larvae versus 30% adult individuals. Seasonal trends in abundance in Mature and New hedges resembled one another, with July representing the 'peak' season and September the low season (Fig. 4.2l). Although hedgeless boundaries differed from this pattern, with a slight upward trend from April through to September GLM showed a statistically significant effect of month, but no effect of boundary type (Table 4.3).

Julida ("snake" millipedes, Class Diplopoda), were more abundant overall in Mature hedges than in either New hedges or Hedgeless boundaries (Fig. 4.2m). Mature and New hedges were broadly similar in patterns of abundance, both showing an upward trend from April to September with peak abundance in September. Hedgeless boundaries by contrast showed peak abundance in April, none in July and showed very low numbers in September (Table 4.1). One boundary had a disproportionate effect on abundance in September: a single Mature hedge was responsible for a spike in numbers, accounting for 75% of the total number of Julida collected for Mature hedges in September. Accordingly, GLM testing showed a statistically significant effect of both month and boundary type on abundance of Julida (Table 4.3).

Psocoptera were found only in hedgerow habitats and were more abundant in Mature hedges than other boundary types in each month (Fig. 4.2n). Seasonal patterns of abundance were very similar between the two types of hedge, with numbers showing an upward trend from April to September, although for New hedges a consistently lower abundance was recorded. One or two Mature hedge boundaries accounted for a high proportion of the total. GLM tests showed a statistically highly significant effect of month and a significant effect of boundary type on numbers of Psocoptera, but no interaction (Table 4.3).

Numbers of Pulmonata peaked in July in all boundary habitat types but abundance was highest in New hedges (Fig. 4.2o). There was evidence of 'clumping', in that abundance tended to be concentrated in a small number of boundaries leading to apparently large variability/standard error. GLM tests showed a highly significant effect of month, but no effect of boundary type for this taxon (Table 4.3).

Siphonaptera (fleas) were represented by only tens of individuals in total (Table 4.1) and were thought to have been transferred to the traps by foraging vertebrates such as shrews (*Sorex* spp.), hedgehogs (*Erinaceus europaeus*) or even birds. They were absent

from samples taken in April, but were present in all boundary types in both July and September (Fig. 4.2p). Numbers were very small and differences were marginal: the GLM returned non-significant results for effect of month, boundary type and interaction (Table 4.3).

The remaining taxa were collected in even smaller numbers (Table 4.1; Appendix B, Tables B1-B4) and no GLM analysis could be performed (see Table 4.3). Polydesmida (flat-backed millipedes, Diplopoda) were present at low levels in both Mature and New hedges but were completely absent from Hedgeless boundaries. Mature hedges showed greatest abundance for all months and in September the majority of abundance was accounted for by just two Mature hedgerows. The 5 least abundant taxa were represented by a total of <5 individuals respectively (Table 4.1). Pseudoscorpiones (pseudoscorpions) were collected from Mature hedges and Hedgeless boundaries, but not in New hedges, and only in September. Orthoptera (grasshoppers and crickets) and Mecoptera (scorpionflies) were confined to New hedges: Orthoptera in July and September and Mecoptera (larval form) in September only. Neuroptera (lacewings) were found only in Mature hedges (single specimens in April and July) and Geophilomorpha occurred just once in a Mature hedge.

4.3.4. Total abundance of invertebrates at ground level/hedge bottom

Figure 4.3 illustrates the mean total abundances (all taxa combined/pooled) for each boundary type and month. Mean abundance values for Hedgeless boundaries were comparable with those for Mature and New hedges, suggesting that they were of equivalent value in terms of total invertebrate numbers at ground-level (see also Appendix B, Table B11). Underlying this was considerable variability in the abundances amongst the individual hedgerows/hedgeless boundaries, with numbers ranging from a peak of 4026, sampled from a New hedge in July, to a low of 114, from a Mature hedge in April. GLM showed that for total numbers of invertebrates there was no significant interaction between month and boundary type (Table 4.4). The test for main effects only showed that month was a highly significant factor in abundance, but boundary type was not statistically significant.

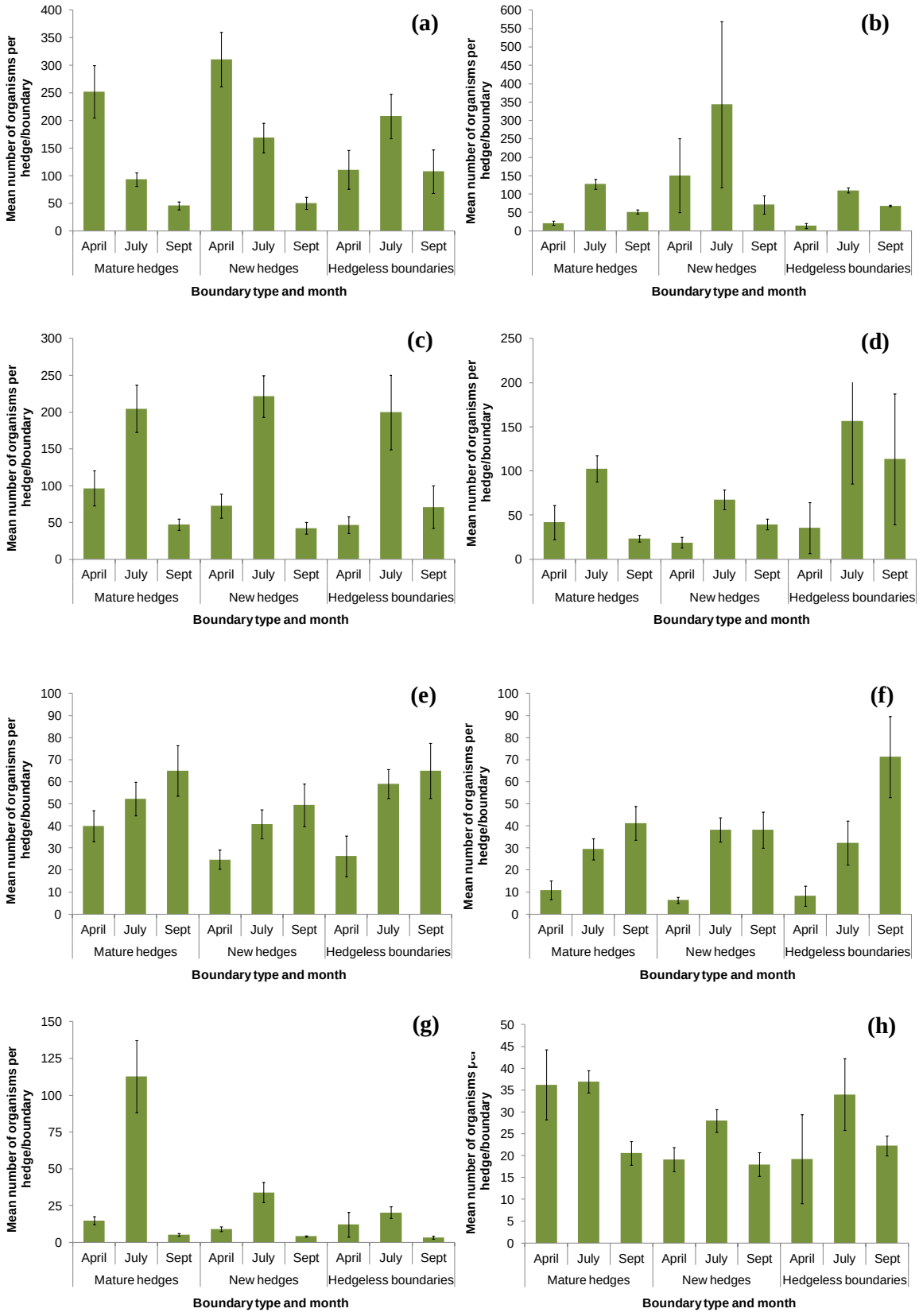


Figure 4.2a-h. Mean abundance (± SE) per hedge/boundary of invertebrates collected by sticky trap at ground level, shown by boundary type (Mature hedges, New hedges, Hedgeless boundaries) and month (April, July, September) in 2011: (a) Collembola; (b) Hymenoptera; (c) Acari; (d) Hemiptera; (e) Diptera; (f) Opiliones; (g) Thysanoptera; (h) Coleoptera

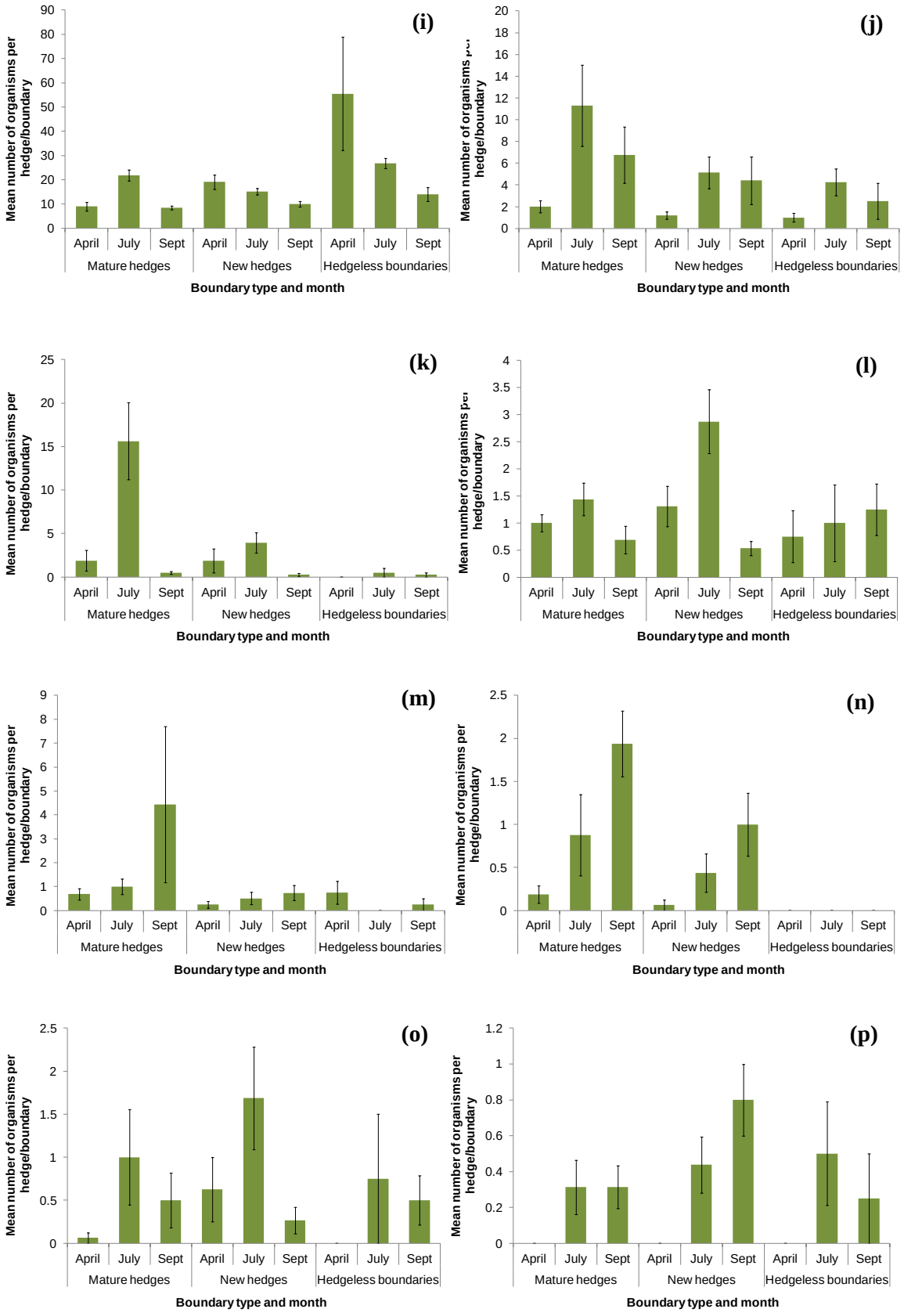


Figure 4.2i-p. Mean abundance (± SE) per hedge/boundary of invertebrates collected by sticky trap at ground level, shown by boundary type (Mature hedges, New hedges, Hedgeless boundaries) and month (April, July, September) in 2011: (i) Araneae; (j) Isopoda; (k) Dermaptera; (l) Lepidoptera; (m) Julida; (n) Psocoptera; (o) Pulmonata; (p) Siphonaptera

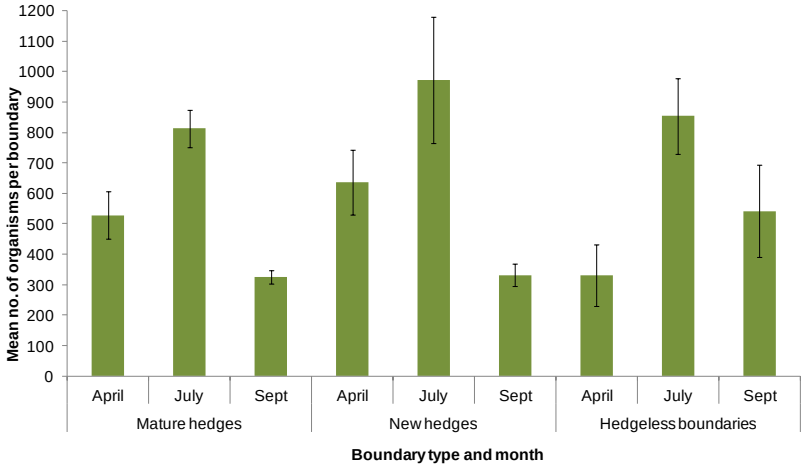


Figure 4.3. Mean abundance (± SE) of all ground-occurring invertebrates (combined) per boundary for each boundary type: Mature hedges (n = 16), New hedges (n = 16), Hedgeless boundaries (n = 4). Invertebrates collected during April, July and September 2011 using sticky traps

Table 4.4. Results of a Generalised Linear Model analysis of the effects of month (April, July, September) and boundary type (Mature hedge, New hedge, Hedgeless boundary) on the total abundance of all invertebrate taxa collected by sticky trapping at ground level

Taxon	Effect					
	Month		Boundary type		Interaction Month* Boundary type	
	Wald χ^2	*p*	Wald χ^2	*p*	Wald χ^2	*p*
Total abundance	8.552	0.014	0.402	0.818	2.135	0.711
(all taxa)	14.899	0.001	0.442	0.802	Main effects only	

4.3.5. Correlations of invertebrate abundance in the hedge bottom with age of hedgerow in years

Spearman's rank correlations were conducted to test for the relationship between age of hedgerow in years and abundance of invertebrates, both in total for pooled taxa and by individual taxon, for each month and for all months totalled. The top 15 most abundant taxa only were included (Table 4.1): remaining taxa were excluded from the analysis because of low numbers. In view of the multiple comparisons, a Benjamini and Yekultieli FDR correction (as described by Narum, 2006) was applied, bringing the threshold significance level down from 0.05 to 0.014.

Age in years was not significantly correlated with total abundance (all taxa) for any month. There was nonetheless a significant to highly significantly positive relationship between age and the abundance of four individual taxa: Coleoptera for all months

combined (Spearman's rank correlation [n = 32 in all cases]: $r_s = 0.549$, $p = 0.001$) and July ($r_s = 0.613$, $p < 0.001$); Diptera for all months combined ($r_s = 0.439$, $p = 0.012$); Psocoptera for all months combined ($r_s = 0.462$, $p = 0.008$); and Thysanoptera for all months combined ($r_s = 0.674$, $p < 0.001$) and July ($r_s = 0.661$, $p < 0.001$).

Correlations, positive and negative, between hedge age and abundance of invertebrate groups were largely weak and non-significant (Appendix B, Tables B12 & B13). Overall evidence for a statistically significant relationship between age in years and abundance of invertebrates was negligible.

4.3.6. Relationships between numbers of individual invertebrate taxa at ground level/hedge bottom

To explore the possibility of using one or more 'indicator' taxa (see Chapter 3), as potential substitutes for other taxa in the boundary assemblages, a series of Spearman's correlations were conducted to test the relationship between numbers of individual invertebrate taxa. As before, taxa with very low counts were not included and an FDR (Benjamini and Yekutieli, 2001) correction was applied giving an adjusted significance threshold of $p = 0.008$. Correlations were conducted on all boundaries for each individual month and also on pooled data for all months and boundaries combined. Key results only are summarised here, but Tables B14-B18 (Appendix B) present the complete dataset.

For all months combined and all three boundary types, Hymenoptera showed the most significant associations overall and their abundance had a highly significant positive, but weak to moderate relationships with numbers of 10 other taxa (Table 4.5). There was a significant, positive relationship between the abundance of Acari and 9 other taxa (Table 4.5); these were largely weak, except for Thysanoptera with which a strong relationship was shown. Numbers of Hemiptera were significantly correlated with 7 taxa, as were Araneae, although these were all largely weak relationships (Table 4.5). Other taxa showed fewer associations overall and abundance of Julida and Psocoptera was not associated with that of any other taxon.

Looking at the hedges only, correlations showed that total numbers of Hymenoptera were significantly correlated with the abundance of 11 of the 15 taxa included in the tests, with a weak to moderate relationship (Table 4.6). Numbers of Acari were significantly correlated with numbers of 9 other taxa and Thysanoptera with 8 others (Table 4.6).

Table 4.5. Spearman's ranked pairwise correlations between the abundance of invertebrate taxa sticky trapped in the hedge bottom: all months combined, all boundaries (n = 107). Top 5 correlates (Acari, Araneae, Hemiptera, Hymenoptera, Thysanoptera) only shown. Values are r_s plus significance values. Significant values are highlighted in bold. A Benjamini –Yekultieli method FDR corrected significance level of 0.008 applies

Taxonomic group	Acari		Araneae		Hemiptera		Hymenoptera		Thysanoptera	
	r_s	p	r_s	p	r_s	p	r_s	p	r_s	p
Acari			**0.356**	**<0.001**	**0.327**	**0.001**	**0.473**	**<0.001**	**0.646**	**<0.001**
Araneae	**0.356**	**0.001**			**0.315**	**0.001**	**0.326**	**0.001**	**0.319**	**0.001**
Coleoptera	**0.541**	**<0.001**	**0.260**	**0.007**	0.140	0.152	**0.465**	**<0.001**	**0.466**	**<0.001**
Collembola	**0.305**	**0.001**	**0.334**	**<0.001**	-0.055	0.575	-0.052	0.597	**0.333**	**<0.001**
Dermaptera	**0.290**	**0.002**	**0.268**	**0.005**	**0.394**	**<0.001**	**0.392**	**<0.001**	**0.396**	**<0.001**
Diptera	0.139	0.154	0.004	0.971	0.194	0.046	**0.366**	**<0.001**	0.105	0.280
Hemiptera	**0.327**	**0.001**	**0.315**	**0.001**			**0.428**	**<0.001**	**0.463**	**<0.001**
Hymenoptera	**0.473**	**<0.001**	**0.326**	**0.001**	**0.428**	**<0.001**			**0.380**	**<0.001**
Isopoda	0.154	0.114	0.047	0.633	**0.360**	**<0.001**	**0.471**	**<0.001**	0.232	0.016
Julida	-0.081	0.410	-0.138	0.155	-0.012	0.900	0.005	0.957	-0.030	0.759
Lepidoptera	**0.275**	**0.004**	0.126	0.197	0.071	0.465	0.246	0.011	0.222	0.022
Opiliones	0.195	0.044	0.037	0.706	**0.269**	**0.005**	**0.414**	**<0.001**	-0.015	0.879
Psocoptera	-0.239	0.013	-0.191	0.048	-0.027	0.782	0.063	0.522	-0.115	0.237
Pulmonata	**0.290**	**0.002**	0.148	0.128	0.202	0.037	**0.365**	**<0.001**	0.105	0.282
Thysanoptera	**0.646**	**<0.001**	**0.319**	**0.001**	**0.463**	**<0.001**	**0.380**	**<0.001**		

Table 4.6. Spearman's ranked pairwise correlations between the abundance of invertebrate taxa sticky trapped in the hedge bottom: all months combined, hedges only (n = 95). Top 3 correlates (Acari, Hymenoptera, Thysanoptera) only shown. Values are r_s plus significance values. Significant values are highlighted in bold. A Benjamini –Yekultieli method FDR corrected significance level of 0.008 applies

Taxonomic group	Acari		Hymenoptera		Thysanoptera	
	r_s	p	r_s	p	r_s	p
Acari			**0.439**	**<0.001**	**0.672**	**<0.001**
Araneae	**0.371**	**<0.001**	**0.361**	**<0.001**	**0.355**	**<0.001**
Coleoptera	**0.519**	**<0.001**	**0.441**	**<0.001**	**0.498**	**<0.001**
Collembola	**0.280**	**0.006**	-0.099	0.339	**0.309**	**0.002**
Dermaptera	**0.336**	**0.001**	**0.405**	**<0.001**	**0.418**	**<0.001**
Diptera	0.095	0.360	**0.319**	**0.002**	**0.113**	**0.277**
Hemiptera	**0.314**	**0.002**	**0.400**	**<0.001**	**0.451**	**<0.001**
Hymenoptera	**0.439**	**<0.001**			**0.376**	**<0.001**
Isopoda	0.121	0.244	**0.475**	**<0.001**	0.193	0.061
Julida	-0.061	0.557	0.042	0.683	-0.062	0.551
Lepidoptera	**0.357**	**<0.001**	**0.275**	**0.007**	**0.297**	**0.004**
Opiliones	0.188	0.068	**0.399**	**<0.001**	0.016	0.874
Psocoptera	-0.248	0.015	0.076	0.461	-0.156	0.131
Pulmonata	**0.296**	**0.004**	**0.378**	**<0.001**	0.128	0.218
Thysanoptera	**0.672**	**<0.001**	**0.376**	**<0.001**		

Hymenoptera showed the greatest number of associations overall where all months were combined. There was only one strong (where the coefficient >0.600) relationship between two taxa: Acari and Thysanoptera. In addition, no single taxon showed significant and strong correlations with multiple taxa in any individual month (Appendix B, Tables B14-B18).

4.3.7. Discriminating between Mature and New hedges using taxonomic abundance at ground level

Candidate predictors of hedge age group membership in the discriminant analysis were the abundances respectively of the top 10 most abundant taxa by month (April, July and September) and for all months combined (see Table 4.1).

Sipina software (Rakotomalala, no date) used to conduct an Improved ChAID Tschuprow Goodness of Split (Rakotomalala, 2005) analysis revealed that the discriminant taxa were not the same for all months. In particular, Hymenoptera (as was the case with results from correlations above) were not identified as a significant differentiator between boundary types despite their apparent super-abundance in New hedgerows.

In April 2011, Improved ChAID analysis indicated that Araneae were the one significant distinguishing taxon, but that their abundance was not a particularly strong predictor or indicator of age group membership for hedges (goodness of split coefficient = 0.250). Based on the abundance of Araneae, 75% of Mature hedges were correctly assigned should Araneae number < 13 and conversely 75% of New hedges were correctly predicted should Araneae number > or = 13.

In July 2011, the ChAID analysis indicated that Thysanoptera were the principle distinguishing taxon and that 88% of New hedges were correctly predicted where numbers of this taxon were < 54, whereas 75% of Mature hedges were correctly predicted where numbers were ≥ 54. The goodness of split/correlation was 0.397, suggesting that Thysanoptera presented a better basis for discriminating between hedge types than any other taxa identified in any other month, but that this discriminatory power was still relatively modest. Other taxa accepted as providing a significantly good split in July were: Coleoptera, whereby 100% of Mature hedges were grouped at ≥ 23.50, but also 50% of New hedges (goodness of split = 0.333); Collembola, whereby 81% of Mature hedges were assigned to the group <111 and 75% of New hedges to the group ≥ 111 (goodness of split = 0.318); and Araneae, whereby 88% of New hedges were assigned to a group corresponding to <21.50 and 62.5% of Mature hedges to ≥ 21.50 (goodness of split = 0.267).

For September 2011, ChAID analysis indicated that there were no significant predictors of assignment to either group (echoing the results of ANCOVA on the taxonomic abundance distributions above).

For all months combined, a decision tree model including Diptera, Coleoptera, Araneae, Isopoda and Thysanoptera was accepted. Analysis showed that numbers of Diptera were the primary predictor of membership to either boundary type, but the goodness of split/correlation coefficient (at 0.112) did not appear particularly strong in itself. Splits in the decision tree showed that Mature hedges fell into the ≥ 24.50 group in 92% of cases. Conversely, only 36% of New hedges could be clearly distinguished from Mature hedges using the suggested split of <24.50. For Coleoptera the suggested split between the groups was calculated at 30.50, with 85% of New hedges falling below this threshold and 56% of Mature hedges equal to or above it. For Araneae, the split was perhaps the most 'balanced' of those taxa accepted by ChAID, whereby the suggested split between the groups was 12.50 with 67% of Mature hedges falling below this level and numbers of organisms in 64% of New hedges coming equal to or above this level. For Isopoda the split was 4.50, with 81% of New hedges falling below this and 48% of Mature hedges above this (still leaving over half grouped with New hedges, however). For Thysanoptera the split was at 35.50, enabling 94% of New hedges to be grouped at numbers below that threshold, but only 29% of Mature hedges grouped at ≥ 35.50, meaning that the majority of Mature hedges fell into the former category.

There were no consistent predictors of hedge age group membership for all months. In both April and all months combined the predictive power of the modelled predictors selected was relatively low. By contrast, the efficacy of the predictors was much higher for July. The mixed results indicate that there is no single good 'indicator' or surrogate group in terms of identifying the distinguishing characteristics of habitats of broad age categories, but also suggesting fundamentally close similarity in the assemblages of both hedge types.

4.3.8. Comparison of invertebrate taxon accretion of different hedge types/boundaries

The investigation of invertebrate abundance above revealed both similarities and differences between the boundary habitats. From the fundamental count data, a number of measures of diversity were calculated to further investigate differences between the faunal assemblages of the boundary habitats.

Taxon accumulation or accretion curves, while not diversity indices as such, can be a useful aid not only to assessing sampling effort but also in comparing and contrasting the

'richness' and heterogeneity of organisms of different habitats. Taxon accretion curves were generated for all months, for the two hedge types only (small sample size of Hedgeless boundaries did not allow comparison), to help visualize trends.

In general terms, as the number of samples increased, the rate at which new taxa were encountered decreased, as the less frequently (or inefficiently) sampled taxa were added. Rates of taxon accumulation differed depending on hedge type. Mature hedges consistently showed a quicker rate of increase than New hedges, reaching their peak sooner and higher, suggesting greater richness and homogeneity amongst Mature hedges. In April, taxon accumulation for Mature hedges reached its asymptote at 14 hedges compared with New hedges whose accretion curves flattened out at 15 (Fig. 4.4a). The accretion rates for Mature and New hedges were most similar in July (Fig. 4.4b). Although taxon accumulation peaked at 15 hedges for the Mature type, it appears as though it had not yet topped out for New hedges. Likewise in September, in contrast to Mature hedges whose taxonomic accretion flattened out at 10 hedges, the accretion rate for New hedges had not reached a plateau, suggesting that further sampling would have added to the tally of taxa for this habitat type (Fig. 4.4c). This suggests lower richness and greater heterogeneity amongst New hedges. A ranked ANCOVA (as described by Quade, 1967 and adapted for SPSS by IBM, no date) indicated significant differences between the taxon accretion rates of Mature and New hedges for April ($F_{1,30}$ = 45.700, p <0.001), July ($F_{1,30}$ = 5.557, p = 0.025) and September ($F_{1,29}$ = 12.519, p = 0.001).

4.3.9. Diversity of invertebrates at ground level - effect of hedge/boundary type on diversity indices

The results from the GLM provided evidence for effects of both month and boundary type on the different measures of diversity of invertebrates (Table 4.7). The model detected a highly significant effect of month on all 6 diversity measures. The Wald chi-squared values and significance levels were lower for effect of boundary type.

Mature hedges generally showed the highest diversity and less variability around median values than the New hedges (Fig. 4.5). Hedgeless boundaries showed more compact ranges/lower variability than either hedge type, but were based on fewer sampling units. Hedgeless boundaries also appear to 'outperform' New hedges in most cases, with the exception of Taxon Richness (Fig. 4.5a). Diversity indices show an upward trend from April through to September in the majority of cases (but particularly marked in New hedges and to a lesser extent Hedgeless boundaries), with peak diversity frequently indicated in September rather than July, which reflects a greater evenness in the

assemblage (Fig. 4.5; Appendix B, Tables B19- B24). In general terms, although boundary type showed a significant effect on measures of invertebrate diversity, the effect of month of sampling was considerably stronger (Table 4.7).

Taxon richness was highest in Mature hedges overall and lowest in Hedgeless boundaries for all months (Fig. 4.5a). Taxon richness varied from a high in July and September, when a maximum of 15 taxa were collected from individual New and Mature hedges, to a low point in April, when only 8 taxa were collected from an individual New hedge. New hedges showed the greatest spread of values in April and September, but Mature hedges had the greatest range in September. Data collected for Hedgeless boundaries was most consistent. GLM showed a highly significant effect of both month and boundary type on taxon richness (Table 4.7).

Berger-Parker values were generally higher for Mature than for New hedges although both had large ranges of values (Fig. 4.5b). Hedgeless boundaries showed consistently higher, and less variable, Berger-Parker values than New hedges and highest median values of any boundary type in both April and September. GLM showed that there was a highly significant effect of month on Berger-Parker values and a significant effect of boundary type (Table 4.7).

There was a large range of Shannon values for New hedges compared with other boundary types (Fig. 4.5c). Hedgeless boundaries were the most diverse boundary type in April, but Mature hedges were the most diverse boundary type in July and September and also showed a smaller range than New hedges. Hedgeless boundaries showed the smallest range of values and appeared to 'outperform' New hedges in terms of diversity. GLM showed a highly significant effect of month and a significant effect of boundary type on Shannon values (Table 4.7).

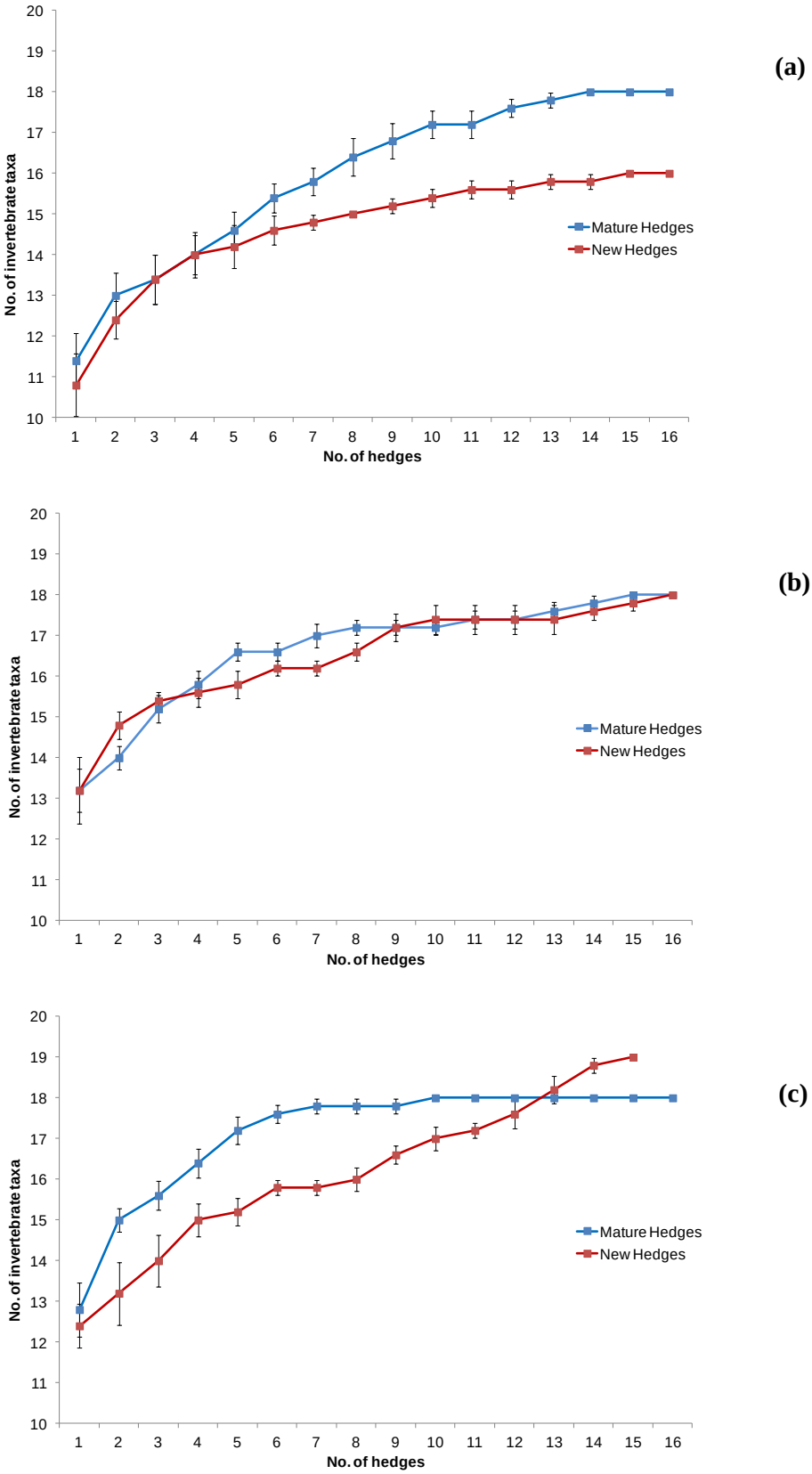


Figure 4.4a-c. Taxon accretion curves showing the cumulative number of ground-occurring invertebrate taxa recovered with increasing number of hedges/boundaries sampled for: (a) April; (b) July; (c) September. Boundary types are: Mature Hedges (n = 16) and New Hedges (n = 16 in April & July, n = 15 in Sept). Vertical lines are ± SE

Table 4.7. Results of a Generalised Linear Model (GLM) analysis of the invertebrate diversity of organisms collected by sticky trap from the hedge bottom, comparing the effect of time (Month: April, July, September) and habitat (Boundary type: Mature hedges, n = 16; New hedges, n = 16*; Hedgeless boundaries, n = 4). Values are Wald χ^2 plus significance values

Diversity measure	Month		Boundary type		Interaction Month*Boundary type	
	Wald χ^2	*p*	Wald χ^2	*p*	Wald χ^2	*p*
Taxon richness	24.396	<0.001	16.728	<0.001	3.930	0.416
Fig. 4.6a	**40.338**	**<0.001**	**16.032**	**<0.001**	Main effects only	
Berger-Parker	27.369	<0.001	8.208	0.017	6.169	0.187
Fig. 4.6b	**51.471**	**<0.001**	**8.107**	**0.017**	Main effects only	
Shannon Diversity	22.645	<0.001	11.337	0.003	6.266	0.180
Fig. 4.6c	**47.207**	**<0.001**	**10.948**	**0.004**	Main effects only	
Heip Evenness	11.674	0.003	7.249	0.027	6.226	0.183
Fig. 4.6d	**27.547**	**<0.001**	**7.294**	**0.026**	Main effects only	
Simpson Diversity	29.657	<0.001	10.465	0.005	6.119	0.190
Fig. 4.6e	**59.782**	**<0.001**	**10.342**	**0.006**	Main effects only	
Simpson Evenness	13.690	0.001	7.799	0.020	6.910	0.141
Fig. 4.6f	**30.180**	**<0.001**	**7.827**	**0.020**	Main effects only	

***in September n=15 due to the loss of one hedge to building work**

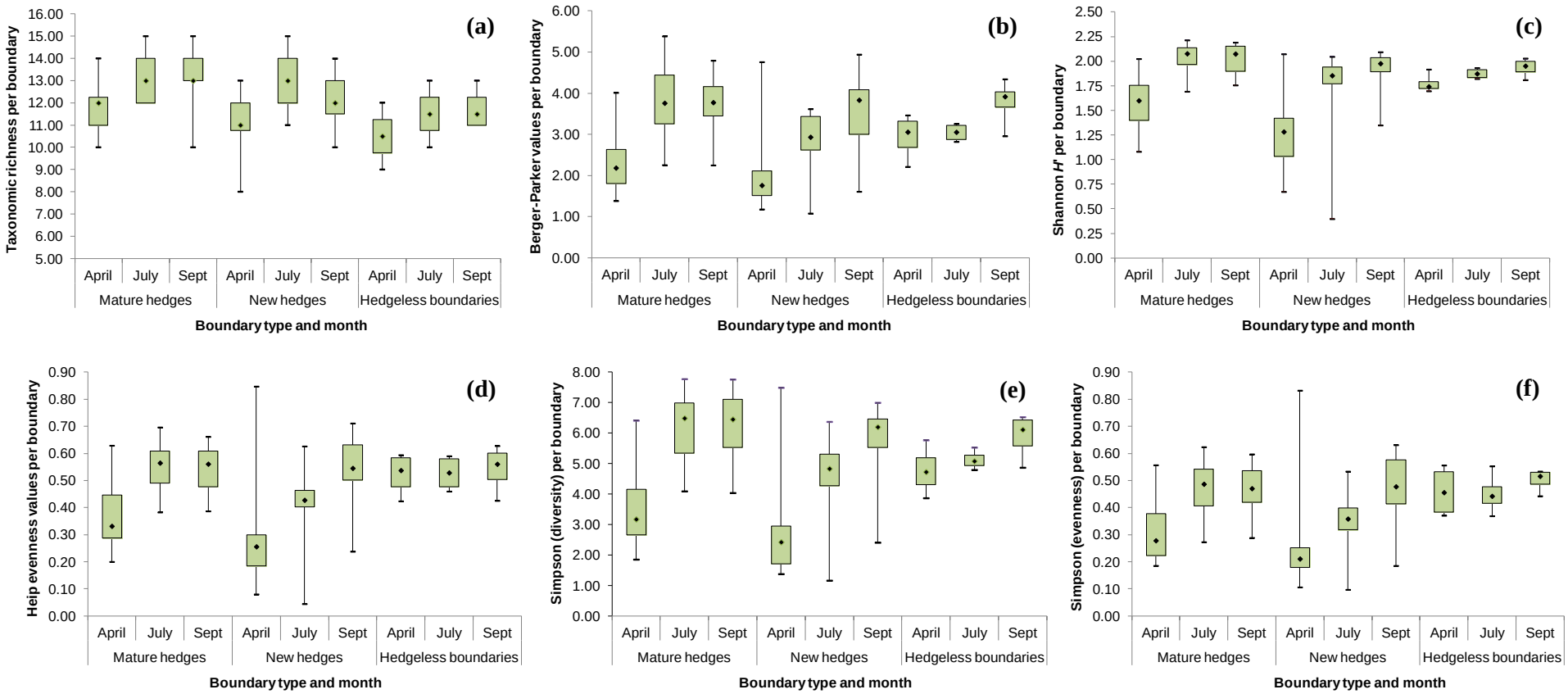


Figure 4.5a-f. Box and whisker chart showing the median (♦), inter-quartile range (shaded box), maximum and minimum values (represented by caps on whiskers above and below box) for each month (April, July, September) and boundary type (Mature hedges, New hedges and Hedgeless boundaries) for the following measures of diversity: (a) taxonomic richness; (b) Berger-Parker (*d*); (c) Shannon indices (*H'*); (d) Heip evenness (E_{Heip}): (e) Simpson diversity (reciprocal – 1/D); (f) Simpson evenness ($E_{1/D}$)

For Heip evenness values (Fig. 4.5d) the pattern is again broadly comparable with other diversity indices measuring for dominance (Berger-Parker), heterogeneity (Shannon) and Taxon Richness. The most obvious attributes are again the large ranges in values of New hedges and a steep upward trend in diversity values from April to September. Mature hedges show greater median values for evenness than New hedges, in April and July but not in September. Hedgeless boundaries were similar from month to month with closely comparable median values and ranges (*i.e.* relatively constrained variation around a relatively consistent central tendency), indicating greater evenness of invertebrate assemblages in habitats without hedges. GLM showed a highly significant effect of month, and a significant (but not as strong) effect of boundary type on invertebrate diversity (Table 4.7).

Simpson values (both for diversity and evenness) showed very similar patterns to other diversity indices (Figs. 4.5e & 4.5f). The median values in fact show a very similar relationship to those of Shannon indices and, although some commentators favour Simpson, here both make equivalent distinctions between boundary types and months. The GLM underlines a similarity between Simpson and Shannon, indicating once more a highly significant effect of month and a significant effect of boundary type on both Simpson diversity and Simpson evenness measures (Table 4.7).

In summary, Mature hedges consistently show greater diversity than New hedges and Hedgeless boundaries consistently 'outperform' both hedge types in April. Hedgeless boundaries generally show the most compact range of values (however, the sample size for hedgeless boundaries was smaller). Although a statistically significant effect of boundary type is evident, month has the consistently stronger effect (Table 4.7).

4.3.10. Correlations between invertebrate diversity in the hedge bottom and age of hedgerow

The results of Spearman's rank correlations (with a B-Y FDR correction of 0.020 applied) for all 32 hedgerows combined (Mature and New) indicated statistically significant positive associations between age in years and 5 of the invertebrate diversity indices in July only, but not for Taxon Richness. The strength and significance levels of correlations were similar for each of the diversity indices, indicating a moderate relationship between the diversity indices and age of hedgerow. The Simpson index values showed the strongest relationship with age in years by a small margin: Berger-Parker (Spearman's rank correlation [n= 32 in all cases]: $\boldsymbol{r_s} = 0.433$, $p = 0.013$); Shannon *H*' ($\boldsymbol{r_s} =$

0.478, p = 0.006); HEIP (r_s = 0.419, p = 0.017); Simpson diversity (r_s = 0.487, p = 0.005); and Simpson evenness (r_s = 0.448, p = 0.010).

Correlations were also conducted to investigate possible associations between invertebrate diversity and age of hedges for the smaller sub-set of 16 New hedges recently-planted under AES, where age in years is known from farm records. Values for diversity/evenness indices were negatively correlated with age, but not at a statistically significant level (Appendix B, Tables B25 and B26).

4.3.11. Alternative indicators of diversity in the hedge bottom

As indicated, the abundance of certain taxa has also been proposed as a means of making the process of biodiversity indication more wieldy, *e.g*. the finding by Anderson *et al.* (2011) that measuring the abundance of parasitic Hymenoptera has good potential as such an indicator. My own investigations had identified Hymenopterans as being a good correlate of overall taxonomic abundance (see 4.3.6), therefore I took a closer look at this group. Hymenoptera were classified into different sub-orders/superfamilies (Appendix B, Figs. B1a-c). The Hymenopteran group was dominated by Formicidae in certain New hedges, whereas the sub-order Parasitica (as defined by Barnard, 2011) was in general a more important component of Hymenopteran fauna. I used the resulting Parasitica group to explore relationships with diversity measures along with the rest of the assemblage.

A series of correlations were performed to investigate the relationship between invertebrate abundance and diversity measures. A number of taxa showed a significant relationship with one or other of the diversity measures. Parasitica were in fact a ‘better’ correlate with diversity measures than Hymenoptera as a whole, but there were actually even 'better' correlates: Hemiptera were significantly correlated with most measures, but relatively weakly on the whole, while Opiliones were significantly correlated with all measures of diversity, showing mainly moderately strong relationships (Table 4.8). Collembola were significantly negatively correlated with all measures, with a moderate to strong relationship in the main. This reflects the fact that Collembola were highly abundant and dominated the assemblage, therefore putting strong downward pressure on diversity scores. There were also some ‘poor’ correlates with diversity: neither Coleoptera nor Diptera were correlated with any measure of diversity (Appendix B, Table B27).

Looking at hedges only, the 'best' correlates with diversity overall overlapped with those for all boundaries, with the exception of Psocoptera. Psocoptera showed a significant, albeit weak, correlation with invertebrate diversity in the hedge bottom for all

measures [n = 95]: Taxon Richness (r_s = 0.305, p = 0.003); Berger-Parker (r_s = 0.303, p = 0.003); Shannon (r_s = 0.394, p <0.001); Simpson (r_s = 0.368, p <0.001); Heip (r_s = 0.276, p = 0.007); and Simpson evenness (r_s = 0.265, p = 0.009). In all relationships, the strength of the correlation and the significance level varied to a greater or lesser degree depending on the diversity measure/taxon (Appendix B, Table B28).

Additionally, two of the most speciose orders, Coleoptera and Diptera, were categorised into families/superfamilies (Appendix B, Tables B5-B10). There were consistently most family groups (taxonomic richness was highest) in Mature hedges for both Coleoptera and Diptera for all months (Table 4.9), although there was no significant difference between Mature and New hedges. The lowest number of families was found in Hedgeless boundaries in every month (from a lower number of boundaries). Although fewer taxa were sampled from Hedgeless boundaries than either hedge age type, they nonetheless scored more highly than the hedges by certain diversity measures. Other diversity measures ranked the boundaries differently depending on month (Appendix B, Tables B29a-c).

Table 4.8. Spearman's rank correlations between abundance of taxonomic groups and diversity measures. Top 5 correlates only shown: Collembola, Hemiptera, Hymenoptera (all), Hymenoptera (Parasitica) and Opiliones. All hedges/boundaries combined for all months combined (n = 107). The B-Y FDR corrected significance level of 0.010 applies

Taxonomic group		Taxon Richness	Berger-Parker	Shannon	Simpson	Simpson Evenness	Heip Evenness
Collembola	r_s	**-0.248**	**-0.575**	**-0.574**	**-0.597**	**-0.572**	**-0.567**
	p	**0.010**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Hemiptera	r_s	**0.305**	**0.283**	**0.353**	**0.313**	0.238	**0.253**
	p	**0.001**	**0.003**	**<0.001**	**0.001**	0.014	**0.009**
Hymenoptera (all)	r_s	**0.407**	0.175	0.189	0.148	0.037	0.066
	p	**<0.001**	0.071	0.051	0.127	0.703	0.501
Hymenoptera (Parasitica)	r_s	**0.461**	**0.374**	**0.391**	**0.348**	0.234	0.230
	p	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.015	0.017
Opiliones	r_s	**0.406**	**0.433**	**0.459**	**0.431**	**0.298**	**0.341**
	p	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.002**	**<0.001**

Table 4.9. Total number of superfamilies/families of Coleoptera and Diptera identified in Mature hedges (n = 16), New hedges (n = 16) and Hedgeless boundaries (n = 4) for April, July, September. Abbreviations: M = Mature hedge, N = New hedge, H = Hedgeless

	April			July			September		
Taxon	**M**	**N**	**H**	**M**	**N**	**H**	**M**	**N**	**H**
Coleoptera	20	15	9	19	18	11	12	11	8
Diptera	18	16	10	28	26	23	24	19	15

4.4. Discussion

In summary, results from sticky trapping invertebrates at ground level provided some evidence of differences between the abundance and diversity in different boundary types. Unfortunately, it was impossible to say unequivocally whether one boundary type was necessarily 'superior' to another boundary type in terms of its ability to accommodate a broad range of invertebrates. There was some evidence for the success of hedge-planting in supporting invertebrate abundance, in that New hedges appeared to be capable of relatively quickly gaining characteristics of Mature hedges. Certainly, in terms of the fundamental structure of the assemblage the results from the taxonomic distribution curves suggested that there was no difference between Mature and New hedges, but that, perhaps unsurprisingly, differences lay between the two hedge types and the boundaries without hedges.

Modelled results from sampling of invertebrates in the hedge bottoms and grassy boundaries indicated no significant difference between overall invertebrate abundance of the different boundary types, although month of sampling was very important. Month was a highly significant factor in the presence of the majority of taxa, although it was clear that for at least some individual taxa boundary type was indeed important in determining numbers. Analysis of diversity showed that boundary type could be a highly significant factor: Mature hedgerows were more diverse in terms of their invertebrate assemblages than New hedgerows or Hedgeless boundaries. Month of sampling was again a very important factor overall determining levels of diversity.

The apparent effect of boundary type on invertebrate diversity but not on abundance corresponds in some respects with other research investigating the effect of age/maturity on the invertebrate fauna of non-crop habitats newly-created or restored under AES. MacLeod *et al.* (2004) detected a positive relationship between invertebrate diversity (Coleoptera: Carabidae and Staphylinidae; and Araneae: Lynyphiidae and Lycosidae) and the age of beetle banks, although not between age and density. By contrast, Pywell *et al.* (2005) reported no effect of habitat (field margin or hedgerow) age on either overall abundance or diversity (using Simpson's measure) of overwintering invertebrates, but more mixed effects on individual taxa. They found that the total abundance and richness of Coleoptera (particularly Carabidae and Staphylinidae) and Araneae were significantly higher in hedgerow habitats compared with the (hedgeless) field margins. Eight species of beetle were recorded in significantly higher densities in

mature habitats compared with four in recently established vegetation. Of these, four showed a conspicuous preference for mature hedges.

Accordingly, in this study differences between the three boundary types ultimately rested on the differences between the relative taxonomic abundances of individual invertebrate groups, and so effects on numbers of individual taxa are discussed here with observations which might help explain the differing responses to space and time. The dynamics of certain groups, notably pest (*e.g.* Hemiptera, Aphididae) or beneficial predator species such as Araneae, Carabid and Staphylinid beetles, and also Lepidoptera are acknowledged to have been well-studied in non-crop farmland/boundary habitats (Barr *et al*., 2005; New, 2005a; Staley *et al.*, 2012a). They continue to be common 'focal groups' (New, 2005a) in research into boundary habitat-invertebrate interactions (*e.g*. Ernoult *et al.*, 2013; Eyre *et al.*, 2013). However, some invertebrate groups appear not to have been so well-studied in recent times (Barnard, 2011), and so, although the ecology and behaviour of these taxonomic groups may be well-understood historically, current populations and distributions, depending on habitat or land use seems to be lacking. It may be that certain taxa are more or even less abundant than we think in certain environments/habitats, irrespective of trapping technique and sampling efficiency.

Dominant in the sticky trap assemblage were several highly abundant groups (notably Collembola and Acari), but there were in fact six taxa for which numbers were so low meaningful statistics could not be performed. They are nonetheless considered, since rarity (sampling effects notwithstanding) is a surprisingly common feature of even highly diverse ecosystems. Typically, assemblages are characterised by a relatively small number of more abundant taxa and many relatively rare taxa (Gaston, 1994). Mouillot *et al*. (2013) indicate that *circa* 50% of coral reef fish species and over 50% of tropical tree species likely to support 'vulnerable functions' are rare, with only one individual ('singleton') per sample. This is not to suggest a direct comparison of agri-environmental conditions with highly diverse tropical systems, but to emphasize that rare taxa form an important part of biodiversity and that there may even be genuinely rare taxa in agro-ecosystems which provide services or functions that cannot be duplicated by other taxa. Some have argued that agro-ecosystems may be less impoverished than generally believed (New, 2005a), but there are indications that even invertebrate taxa assumed to be abundant and diverse may be in serious decline (Brooks *et al*., 2012). For instance, Benton *et al.* (2002) observed that certain taxa were 'rare' in suction sampling on farmland, *e.g.* Neuroptera.

4.4.1. Mixed responses of individual taxa to boundary type

There was mixed evidence of an effect of boundary type on numbers of individual invertebrate taxa at ground level. In total, only 8 (out of 16) taxa included in the GLM showed a significant response in numbers to a particular boundary type. For Dermaptera, Isopoda, Julida, Psocoptera and Thysanoptera, the presence of a Mature hedgerow determined significantly higher numbers than the other boundary types. By contrast, Araneae and Hemiptera were found to be significantly more abundant in Hedgeless boundaries than either Mature or New hedgerows. Only Hymenopterans (composed principally of Formicidae) had significantly greater abundance in New hedgerows than in any other boundary type. This means that for the abundance of the majority of taxa collected in the hedge bottom boundary type appeared to be essentially irrelevant, or could not be adequately tested because of low numbers trapped. More specifically, the presence of a hedgerow, whether mature or more recently planted under AES, was not, at least in statistical terms, a key factor in the numbers of organisms in each taxon. By contrast, the majority of taxa showed a significant effect of sampling month, with the exception of Coleoptera and Siphonaptera.

The following discussion deals with individual taxa by boundary type, and the effect of month is also considered in the context of what is known about the ecologies of respective groups. Influences of explanatory variables for which data was also collected, and which potentially underlie effects of boundary type and month highlighted here, are discussed in Chapter 6.

4.4.2. Taxa exhibiting greatest abundance in Mature hedges

Of the five invertebrate taxa which sticky trap catches showed to be particularly well-supported by Mature hedges, **Dermaptera, Isopoda and Julida** are fundamentally similar in their ecological requirements. All three are said to prefer sheltered and confined, humid microhabitats, such as soil, litter, rotting vegetation or under bark (Wallwork, 1970; Jones & Jones, 1984; McGavin, 2001), avoiding conditions of low humidity because of vulnerability to dessication (Coleman *et al.*, 2004). Such conditions were likely to have been encountered in the larger, more sheltering Mature hedges.

In addition, all three taxa have broadly detritivorous or saprophagous feeding requirements. Dermaptera feed predominantly on dead and decaying vegetable and animal matter, with some predation and some consumption of living vegetation (Gullan & Cranston, 2005). Isopoda also prefer to feed on decomposing vegetation (Hopkin, 1991).

Dead plant material, particularly leaf litter and decaying wood are the main food sources for many Diplopoda (Wallwork, 1970). This might mean they are more likely to find favourable foraging conditions in Mature habitats, where the woody element of the hedgerow is better developed, where the verge or grassy element is longer established and animal and vegetable population processes, trophic structures and nutrient cycles may be better established than in newer habitats (Dowdeswell, 1987). Also, a well-developed woody element in a Mature hedge may well prevent loss of leaf litter at the hedge base. The preference for bark and decaying wood in the case of Isopoda and Dermaptera means that Mature hedges with a more developed woody element would provide more favourable conditions than New hedges. By contrast, Hedgeless boundaries, lacking woody habitat, would be suboptimal.

Dermaptera showed a significant interaction between boundary type and month. The interaction appears to be mainly accounted for by a conspicuous spike in numbers of Dermaptera in July in Mature hedges (Fig. 4.2k). A possible explanation for the summer spike is that dispersal, once young have developed, takes place about July (Jones & Jones, 1984). Overall their abundance was not high, fitting with Wallwork's (1970) view of them as having a 'sporadic' distribution and low densities.

The majority of Julida were found 'clumped' in one single Mature hedgerow. Some Julida species have a preference for acid soils (Wallwork, 1970) and the soil profile of this one hedgerow is known to be acidic from work on soil pH (not analysed as a factor in multivariate analysis due to overall lack of differentiation between pH levels). Julida appeared to be otherwise relatively sparsely distributed. They are presumed to be less likely to be active/dense on the surface itself than in the soil and are therefore probably less liable to be trapped by sticky trapping than, for instance, a soil extraction technique.

Twice as many **Psocoptera** were collected from Mature hedges as from New hedges. None at all were collected from Hedgeless boundaries, where a woody element was lacking. Psocoptera are said to be found in a very wide range of terrestrial habitats, including nests of birds, bees and wasps, but they are particularly abundant on bark and foliage of trees and shrubs where they consume microflora such as algae, lichens and fungal spores (New, 2005b; McGavin, 2001; Barnard, 2011). New (2005b) indicates that ground litter is a 'generalised' psocid habitat and this would account for the presence of Psocoptera at ground level rather than exclusively within the woody part of the hedgerows, despite their familiar name 'barkflies'. However, numbers were generally low and this reflects the fact that, although some British species are found on grasses and other low

vegetation, their preference is for arboreal habitats (New, 2005b). They are generally presumed to fly rather little (New, 2005b), and their 'reluctance' to move may affect samples where capture rates depend on the activity of invertebrates in the environment. Their relatively sedentary nature could account partly for the relatively low catches on the sticky traps.

It is unclear why psocids should peak in number in September, although this may have to do with the accumulation of leaf litter and the greater presence of some of their main foodstuffs (moulds and fungi) during the autumn. This is an understudied taxon in Europe, including in the British Isles, and there appears to be a continuing deficit of information on expected abundance or dispersal in the environment (Barr *et al.*, 2005; New, 2005b; Staley *et al.*, 2012a).

Thysanoptera were also more likely to be found in Mature hedges with a conspicuous peak in abundance in July. Barnard (2011) indicates Thysanoptera can be present in huge numbers in favourable conditions and total catches on sticky traps did indeed run into the thousands in Mature hedgerows, particularly from one location. At Swallow, the crops were all cereals in 2011 and it is therefore tempting to speculate that these numbers were boosted by the widespread *Limothrips cerealium* (grain thrips or thunderfly), which feeds on grasses, breeds in the ears of cereal crops, and emerges in vast numbers when the crop is ripe (McGavin, 2001). This may account at least in part not only for the spike in numbers of in July, but also the sharp drop in numbers in September once crops have been harvested and vegetation begins to die back. Thysanoptera also thrive under warm, humid conditions and these were weather conditions that prevailed in July 2011. Although the majority of thrips species are known to be flower- , grass- or leaf-feeders, other species are predatory or feed on fungal spores often concealed from view, *e.g.* under leaf litter, bark or host fungi (Barnard, 2011). Favourable conditions for Thysanoptera may be more readily encountered in Mature hedges rather than New hedges or Hedgeless boundaries.

It seemed that a common ecological requirement of those taxa found in greatest abundance in Mature hedges was the presence of decaying organic matter and in particular leaf litter. Studies by Maudsley *et al.* (2002) and Pywell *et al.* (2005) have similarly indicated the importance for the abundance of certain invertebrates (Coleoptera and Araneae) of leaf litter and biomass of vegetation, which tends to accumulate with time as boundary habitats grow. Leaf litter appears to be important in providing the right conditions (*e.g.* shelter from adverse weather, living space within the soil structure,

drainage, food resources *etc*) for a range of invertebrate organisms, not only detritivores. It is assumed that accumulations of leaf litter and plentiful decaying vegetation are more likely to occur and remain in place under the sheltered conditions provided by a well-established hedgerow. However, volumes of leaf litter were not measured directly in this study.

4.4.3. Taxa exhibiting greatest abundance in New hedges

Numbers of **Hymenoptera** were significantly higher in New hedges and a significant interaction between month and boundary type was shown. This effect reflected a particularly conspicuous spike in abundance in July in New hedges, where the Hymenopteran fauna were dominated by Formicidae. The majority of Hymenoptera were in fact collected in just one hedgerow. If this one 'outlier' were removed from the dataset and the value replaced by the mean for New hedgerows, then Hymenoptera would actually be less abundant in New hedgerows than in Mature hedgerows. This is another example of the significant 'clumping' or aggregations of populations, which can be a feature of ecological count data (Southwood & Henderson, 2000; Fowler *et al.*, 1998). This study does not suggest that Formicidae are rare or endangered animals on farmland or indeed in hedgerows in general, but taken as a model of what can occur in natural populations, it points to a potential threat to the persistence of organisms where high numbers appear to be confined to a restricted number of suitable habitats and there is rather sparser dispersion through the majority of habitats.

The biological explanation for the high abundance of Formicidae in this particular hedgerow is rather unclear, but possibly has to do with the sandy-soiled hedge bottom and sparse vegetation. Wallwork (1970) reports that, in common with many other taxa, ants select warm, sheltered, moist conditions. However, it may indicate that large colonies can flourish in sandy soils and that some apparently avoid or move away from shady sites and those with accumulations of organic matter. Previous hedgerow work by Deeming *et al.* (2010) using pitfall traps also observed significantly larger numbers of Formicidae in a sandy soil associated with three boundaries newly planted (~3 yrs) under AES. Since sticky traps do not require digging in, disturbance through the so-called "digging-in effect" (Greenslade, 1973) observed from pitfall trapping is less relevant to the current study, although it may be that some sort of disturbance of the population took place, perhaps as a result of field activities, triggering greater activity. Alternatively, there may have been ant nests in the transect, with large numbers of ants perhaps suggesting a migration to form a

new colony. The result could also suggest that really favourable conditions for Formicidae are not as common in agro-ecosystems as we might assume.

4.4.4. Taxa exhibiting greatest abundance in Hedgeless boundaries

Mean numbers of both **Araneae** and **Hemiptera** were significantly higher in Hedgeless boundaries than in either of the hedge types and month of sampling was a highly significant determinant. Wallwork (1970) reports that Araneae are frequently found in 'open' situations and grasslands often support a rich spider fauna. Many families are ground-running and/or ground-living in a variety of open habitats in grassland and grassy tussocks, heathland and scrub, as well as woodland, but only Dictynidae are expressly associated with hedgerows by Jones-Walter (1989). It is concluded that Hedgeless boundaries and New hedges (with their relatively underdeveloped woody elements) could be considered more 'open' habitats than Mature hedges and this impacted on spider abundance. It is unclear why numbers of Araneae peaked in April as opposed to July. Perhaps this was a period of high activity/density of certain species as they dispersed after a particularly cold, harsh winter 2010/2011 (Black, 2011; Met Office, 2011). Pywell *et al.* (2005) reported that overwintering Araneae were in fact significantly more abundant in hedgerow boundaries as opposed to hedge-free field margins. The winter period was however not included in the sticky trap sampling.

Although not quantified precisely, large numbers of ground-running spiders, notably Lycosidae (wolf spiders), and also Thomisidae (crab spiders) were observed in all habitats. It was also noted during analysis that Linyphiidae (money spiders), some species of which are known to be highly dispersive (Jones-Walter, 1989), appeared to be well-represented in the samples. Some Araneae rely on varied and sometimes complex vegetation structure to support a large range of web architectures (Agnarsson, no date). Botanical complexity sustains higher abundance of Araneae and higher diversity (Foelix, 1996). Reduced management intensity and increased vegetation complexity can help conserve invertebrate diversity, whereas cutting of vegetation can negatively affect web-building spider populations (Diehl *et al.*, 2013). The Hedgeless boundaries were not subject to the same cutting regimes as the verges associated with hedgerows and so this may also have helped them provide more favourable conditions for Araneae, and their prey.

Hemiptera were also significantly more abundant in the grassy boundary habitats where no hedge was present, particularly during July. Both herbivorous and predatory sub-

groups were present, but catches tended to be dominated by aphids (Aphididae), Psyllidae (plant lice) and Cicadellidae (leafhoppers); other Heteropteran groups (notably Anthocoridae, Lygaeidae, Miridae, Nabidae and Tingidae) were found in lower numbers in the Hedgeless boundaries. This might suggest that Hemiptera responded well to the abundance of grassy vegetation in the hedge-free habitat and because of the lower intensity of cutting, groups such as aphids, tended to thrive (as observed by Diehl *et al*., 2013).

Regarding the effect of month on numbers, Hemiptera show a fairly 'conventional' summer peak in numbers in July – aphids, for example, gradually increase during late spring and summer (Chinery, 2007). Araneae feed on a wide range of invertebrates, but can contribute to for instance aphid suppression (Holland *et al*., 2012; Diehl *et al.*, 2013). Prey-seeking behaviour is likely to have influenced the dispersal of Araneae, including Lyniphiidae, which are known to be effective aphid predators (GWCT, no date a). This predator-prey association may form part of an explanation why the highest mean numbers of Hemiptera and highest mean numbers of Araneae are found together in Hedgeless boundaries. Hemipterans are of course also predated by other taxa that did not seem to have a significant preference for Hedgeless boundaries.

4.4.5. Taxa for which there was no effect of boundary on abundance

Acari and **Collembola** are both large, diverse groups, widely distributed throughout ecosystems in high numbers in many different habitats (Jones & Jones, 1984; Coleman *et al*., 2004; Hopkin, 1997 & 2007). Both have rather generalist requirements and can adapt their feeding and habitat space needs as required which might account at least partly for their apparent widespread success (Coleman *et al*., 2004), and for their lack of preference for a particular boundary habitat type. As indicated repeatedly for other taxa, leaf litter seems to figure strongly in their apparent basic requirements, but also other detritus, decomposing vegetable matter, fungal hyphae and spores, live plant material, algae, bacteria, carrion, pollen and even faeces (Wallwork, 1970; Hopkin, 2007) and for the parasitic Acari, appropriate invertebrate and vertebrate hosts. Mature hedges did not however provide especially favourable conditions, as they had for other taxa with similar requirements (see 4.4.2). An Austrian study examining the effects of habitat age (grassy fallow) on the abundance of predatory mites (Acari), found that density of Acari did not increase with increasing maturity, but that populations in younger habitats were found to exceed those in older habitats (Wissuwa *et al.*, 2012).

Some research suggests that farmland hedgerows are important refugia for Collembola (*e.g*. Alvarez *et al.,* 2000; Frampton *et al.,* 2007). Wallwork (1970) indicates however that the influence of type of habitat is an indirect one, perhaps exerted through effects on soil type and soil pore space, which would account for the lack of preference for any particular boundary, with or without hedge.

April was the peak month for numbers of Collembola in hedgerows, as opposed to a July peak for the Hedgeless boundaries. Jones & Jones (1984) indicate peaks in breeding in May and September, whereas Wallwork (1970) indicates January and July. The April peak seen in sticky trapping may correspond approximately to the expected spring peak, but no spike in numbers was seen in either July or September. Both Hopkin (2007) and Coleman *et al.* (2004) point to the fact that Collembola can experience explosive population growth under suitable conditions, irrespective of season, and give off aggregation pheromones which may be more important than either habitat variables or food resources in determining their abundance in any one place. Acari were conspicuously abundant in all boundary types in July: seasonal activity/density of Acari is known to peak during summer months, but sticky trap samples die not reflect reportedly high activity in spring and autumn (Coleman *et al.,* 2004).

Diptera were found to be affected by month, with abundance rising from April through to September, but showed no preference for hedgerows of either age type over Hedgeless boundaries. Their diversity as an order – there are ~7000 species in Britain (Chandler, 2010) - combined with good dispersal ability, probably explains the lack of any apparent preference for one of the three habitats when taken as a group. Correlations did, however, suggest a positive link between numbers and increasing maturity of habitat. Sciaridae, which formed a substantial component of Dipteran catches, are closely associated with decomposing wood (Godfrey, 2003), and probably influenced the apparent preference for more mature hedges.

Along with Mycetophilidae, Sciaridae form a group known familiarly as ‘fungus gnats’ (Freeman, 1983; Oosterbroek, 2006). Basic conditions for many of these groups, notably damp soil, leaf litter and decomposing vegetation with fungal growth, can be met in a variety of habitats. As autumn approaches and vegetation dies off conditions should improve for such organisms, which may account for a peak in numbers of Diptera in September.

Phoridae, the largest family of flies in GB (Barnard, 2011), were also well-represented in the sticky trap samples. They are known to be ‘cosmopolitan’, often

parasitoid, adaptable and found in a wide range of habitats and prey/hosts, such as Araneae, Hemiptera (notably aphids) and Pulmonata, decomposing matter or fungal substrates (Oldroyd, 1970; Barnard, 2011). Phoridae are also reputed to be particularly 'tough': their larvae have been found to survive in long-dead bodies and even in tissues preserved in formalin (Oldroyd, 1970; Barnard, 2011). They therefore seem well-equipped to survive in potentially harsh agro-ecosystems, where there is often physical or chemical 'disturbance', even in non-cropped areas.

The apparent importance of Phoridae and Sciaroidea in sticky trap samples accords with results from other terrestrial ecosystems. Nielsen & Nielsen (2007) reported the predominance of Sciaridae, Cecidomyiidae and Phoridae in their samples of the Dipteran fauna of beech stands versus arable fields. Phoridae could make up over 20% of Dipterans sampled in arable fields and that numbers of Sciaridae responded positively to anthropogenic disturbance likely to be experienced in the arable environment. Nematocerans, which include Sciaroidea, have been reported to make up the vast majority of Dipteran numbers (>60%) in arable environments (Nielsen & Nielsen, 2007). My study found that Phoridae could make up well over 30% of Dipteran fauna in July and although Nematocerans did indeed account overall for >60% of fauna in April and September, they were far outnumbered by Brachycerans in July. Composition of the Dipteran assemblage however depended not only on month but also boundary type (Appendix B, Tables B5–B7).

Lepidoptera, represented largely by larval stages, were infrequent in this study. Lepidoptera were also seldom recorded by Deeming *et al.* (2010) using pitfall traps to sample the invertebrate assemblages of arable hedgerows. Admittedly, Lepidoptera as a whole could not be considered truly ground-active as such, activity at ground level is well-documented, *e.g*. Carter (1984) described a number of species whose larvae feed on roots and tubers of arable crops or sever stems (cutworm larvae of some Noctuidae), also Micropterid larvae are free-living ground dwellers in moist environments, feeding on fungal hyphae (Resh & Carde, 2003; Barnard, 2011). On this basis, while some might have been wind-blown from taller vegetation, not all Lepidopterans on the sticky traps could be regarded as random captures.

It is known that farmland butterflies are in decline, and that both specialists and, perhaps more alarmingly, generalist species are decreasing (Defra, 2012; Defra/JNCC, 2014). Losses to butterfly populations are likely to be a contributory factor in the low abundance seen in this study. Similar downward trends are reported amongst farmland

moths (Fuentes-Montemayor *et al.*, 2010), which made up almost all adult Lepidoptera collected on sticky traps. Fuentes-Montemayor *et al.* (2010) found that the presence of hedgerows did not enhance moth populations, whereas the presence of rough grassland and scrub increased numbers significantly. Results from the sticky traps suggest that hedgerows are not optimal habitats for Lepidoptera. Despite the much emphasized shelter effect of hedgerows and an apparent preference for mature hedges (Barr *et al.* 2005), a conspicuously positive effect of hedgerows on Lepidoptera numbers in the hedge bottom was not seen. There was, however, no indication that the grassy hedgeless boundaries were preferred. Fuentes-Montemayor *et al.* (2011a, 2011b) concluded that AES options, including hedgerows, were not meeting the needs of Lepidoptera, and it seems that although these organisms may be widespread, they are not abundant in the farmed environment, despite agri-environmental interventions.

Opiliones were also unaffected by boundary type and apparently unresponsive to the presence of a hedgerow, irrespective of age, whereas abundance increased over the sampling period, peaking in September. The majority of British Opiliones prefer environments where leaves accumulate and may tend to be more abundant in woodland than in more open habitats (Wallwork, 1970). It might therefore be assumed that they would be more abundant in woody habitats. They are generalist predators, feeding on a variety of ground-dwelling invertebrates, but will also feed on carrion and decomposing vegetable matter (Wallwork 1970; Richards, 2010). A densely vegetated grassy boundary may be as likely to offer such a generalist predator these conditions as a hedgerow.

The peak in numbers caught by sticky trap in September fits the annual cycle of many Opiliones, which mature in the autumn and become most 'visible' (Richards, 2010). Unpublished data collected in 2007/2008 by the author of this study using pitfall traps also showed that Opiliones peaked in numbers in September and were significantly more abundant in Mature hedges than hedges more recently established under AES, but sticky trap catches did not reflect this preference.

Pulmonata (snails) are regarded as common and widespread and in agricultural fields may run into thousands per acre (Wallwork, 1970; Cameron, 2003), but proved rather rare using sticky traps. Smaller specimens (≤ 5mm) predominated and larger specimens are likely to have been excluded by the protective metal mesh. Their generally low numbers are likely to be due to ineffectiveness of sampling method compared with, for instance, pitfall trapping, and they appear almost as 'incidental'.

4.4.6. Taxa exhibiting no effect of boundary type or month

Coleoptera were most abundant in Mature hedges, but not by a considerable margin and results did not suggest boundaries with hedgerows were favoured over boundaries without. Correlations did however show that numbers of beetles as a whole increased with age of habitat. In addition, whilst abundance was greatest in July in all three boundary types, no effect of month was shown. Pywell *et al.* (2005) found that Coleoptera were generally significantly more abundant in hedgerows than field margins, but showed an association with habitat age in the case of a relatively small number of species only. Kromp (1999) indicated that age *did* have a significant effect, at least on the abundance of Carabids; in this instance newly established hedges supported larger populations than older hedges. Some further analysis at beetle family level (Appendix B, Tables B8–B10) would support this view because Carabids were more common in New hedges and even preferred Hedgeless boundaries at certain times.

It is unclear why both month and boundary type had no impact on the abundance of Coleoptera, although some research suggests that hedgerows/boundaries are generally less preferred than fields themselves (Moreby & Southway, 2001). Pywell *et al.* (2005) cite good dispersal ability as a factor in their results. It may indeed be that as a consequence of being a large, highly speciose (~4,000 species in Britain), highly abundant and ubiquitous group (McGavin, 2001; Barnard, 2011), they are adapted to a large range of ecological niches taken as a group. Coleman *et al.*, (2004) also indicate they are 'cosmopolitan', catholic feeders. Fry & Lonsdale (1991) suggest that among beetles the range of food sources is perhaps greater than other insect orders, with the implication that this enables them to be widespread. Joyce *et al.* (1997) conducted a 'knock-down' study on hedgerow invertebrates which illustrated the resilience and rapid dispersal ability of Coleoptera as a group. After spraying pyrethroid insecticide into the hedgerow and monitoring recolonisation rates, Coleoptera, particularly Carabidae, Chrysomelidae (leaf beetles) and Staphylinidae, proved to be the fastest recolonisers, reaching numbers significantly greater than pre-spray levels. By comparison, none of the other major taxa (Araneae, Diptera, Hemiptera, Hymenoptera) had returned to pre-spray levels within a 30-day period. Joyce *et al.* (1997) suggested that Coleoptera recolonise first because they are essentially insects of the ground and are opportunistic feeders capable of switching food sources. Being such a varied and adaptable group, with many ground-dwelling members, they seem able to thrive and disperse in a range of ground-level conditions throughout the seasons.

Siphonaptera did not respond to any particular boundary type, which suggests that their host species (mammals and birds) also showed no strong preference for a particular habitat in this study. However, in a sense they were an incidental by-catch, collected in relatively low numbers.

4.4.7. 'Rarity' amongst invertebrates at ground level

There were a number of taxa which were sampled at very low levels and could have been seen as 'rare'. A few words relating to their apparent rarity are appropriate, since ecological communities are characterised by their many rarities as much as their more abundant taxa (Gaston, 1994; McGill *et al.*, 2007). Rare taxa are prevalent in invertebrate assemblages with many being represented only by a single individual, so-called 'singletons' (Magurran, 2004). An alternative explanation of low densities of animals would be that the taxon is known to be abundant in certain habitats, but is simply rare at the location (or indeed in the habitat) being sampled (Magurran, 2004).

The issue of sampling effectiveness is also relevant, since different sampling methods will inevitably give different impressions of rarity, which is also dependent on the ecology/behaviour of the organisms. Southwood & Henderson (2000) acknowledge the difficulty of devising an "all-species method" of capturing invertebrates, although inevitably some techniques will be better suited than others to collecting certain taxa.

Only one specimen of **Geophilomorpha** was sampled. This group is however essentially subterranean, living in the soil surface, and therefore rarely coming above ground (Wallwork, 1970; Jones & Jones, 1984; Coleman *et al.*, 2004). Their low abundance is thus not necessarily an indication that they are of low densities in the habitats sampled, but that the sticky trapping technique was not well-suited to sampling them. For targeted sampling, soil coring in combination with a Berlese-Tullgren funnel would be more useful for catching smaller species. Hand searching, leaf litter sifting and pitfall trapping are variously used as collection techniques for Chilopoda and other myriapods generally (Zapparoli, 2011). Interestingly, Geophilomorpha were found at very low densities in pitfall trapping undertaken by Deeming *et al.* (2010). Also, despite using an active searching method for Geophilomorpha, Blackburn *et al.* (2002) collected relatively modest numbers (the equivalent of 3 per hectare). They may be less common than thought, or at the very least less apparent.

Three specimens of **Mecoptera** were trapped in one New hedge. Likewise, Deeming *et al.* (2010) found very low numbers of Mecoptera via pitfall trapping in

farmland hedges, but confined to mature habitats. Mecoptera are scavengers, found generally in damp wooded or shady areas where there is plenty of vegetation, rough grassland and woodland margins, often among brambles (McGavin, 2001; Chinery, 2007; Barnard, 2011). Hedgerows are a known habitat of the Common Scorpion Fly (*Panorpa communis*) (Gibbons, 1995), but as (albeit weakly) flying insects they may avoid ground level traps.

Sampling technique may have accounted in part for the occurrence of so few individuals. However, generally low abundance, or at least low apparency, of these organisms could be a factor. Information on their distribution appears to be lacking, but irrespective of general abundance, the indications are that Mecoptera are hard to find (Wallwork, 1970; Barnard, 2011). Deeming *et al.* (2010) indicate that most Mecoptera were caught in August and so month of sampling may be another factor in accounting for the low numbers found in this study. Stelzl & Devetak (1999) reported the sensitivity of Mecoptera to the chemical and mechanical disturbances in agro-ecosystems: they may therefore be genuinely unsuited to the arable environment**.**

Neuroptera were represented by only two specimens, both collected from Mature hedges. There are numerous species with woodland or deciduous tree and shrub habitat preferences (Plant, 1997). Neuroptera are weak fliers and therefore at risk of involuntary dispersal by the wind, which is why they are adapted strongly to more sheltered woodland, rather than the comparatively more open and exposed habitats such as farmland hedgerows (Stelzl & Devetak, 1999). Method of sampling probably also contributed to the impression of rarity.

Plant (1997) recommends various methods for sampling Neuroptera at ground level, including pitfall traps and water traps. These methods were used by Deeming *et al.* (2010) and Farrow (2011, unpublished undergraduate thesis) respectively to trap invertebrates from a selection of hedgerows on University of Lincoln farmland, but only captured very small numbers of Mecoptera overall and not a single Neuropteran specimen. There is little indication of true densities in the farmed environment, although they are said to be abundant in woodland, gardens and grasslands (Plant, 1997; Royal Entomological Society, 2012).

Only three **Orthoptera** were caught by sticky traps, but while some Orthoptera can be very rare or limited in geographical range, others such as grasshoppers and ground hoppers can be widely distributed (Tilling, 1987). Given the size and movement of some Orthoptera, they were probably unlikely to have penetrated the protective wire around the

sticky traps. Low densities in the habitats sampled would therefore seem an improbable explanation.

Polydesmida are reportedly relatively inactive and restricted to litter layers (Wallwork, 1970). Their general inactivity may have contributed to their low numbers, although sampling effect is also implicated. Unpublished data collected in 2007/2008 by the author using pitfall trapping indicated that Polydesmida were moderately abundant, certainly not as 'rare' as catches from sticky trapping would suggest.

The low frequency of **Pseudoscorpiones** in sticky traps tallies with their cryptic behaviour, generally low abundance and scattered distribution (Wallwork, 1970; Coleman *et al.*, 2004). Dennis *et al.* (2001) sampled arachnids of upland grasslands by pitfall trapping and vacuum sampling, but neither method yielded large numbers of Pseudoscorpiones, suggesting this taxon is sparse in livestock farming environments, if not in agro-ecosystems in general. No Pseudoscorpiones were sampled during over a year of monthly pitfall trapping conducted by Deeming *et al.* (2010). Indeed, Wallwork (1970) indicates that they may be more regularly sampled in forest habitats where forest leaf litter and bark offer the suitably cryptic small crevices they like to inhabit (Coleman *et al.*, 2004). Although hedgerows are a woody habitat and often compared with woodland, it would seem that hedges of agro-ecosystems may not be the optimal habitat for Pseudoscorpiones.

It was uncertain to what extent very low numbers of these taxa were attributable to an effect of sampling or a real result of the pressures they face in arable farmland, pressures which ecological restoration under AES may be unable to mitigate. Further focused sampling using alternative methods and extending the sampling season would help resolve this.

4.4.8. Response of invertebrate diversity at ground level to boundary type

Quantifying biological diversity accurately is a major preoccupation for ecologists and conservationists throughout the world. Many measures of diversity already exist, and more are being added, with the result that no single measures are used consistently for particular habitats, leading to difficulties when comparing results of different surveys (Magurran & McGill, 2011).

For comparison, inclusion of a selection of indices in studies of ecological diversity is even recommended by some commentators, because of the way different diversity indices 'weight' different aspects of the assemblages measured, *e.g.* Simpson is less

sensitive to richness than Shannon. The different weightings can lead to different results. Hence, in this study, it was apparent that although overall diversity was shown to be superior in Mature hedges, some indices suggested a closer similarity with New hedges than others.

The "iconic" (Magurran, 2004) measure of species richness was converted in this study to "taxonomic richness" due to the high level analysis and used in addition to other diversity measures, giving a perspective of the effects of boundary type on different aspects of diversity, encompassing dominance, evenness and heterogeneity. A measure of taxon accretion was also used to gauge diversity and showed significant differences between the two hedge types with a significantly higher accretion rate in Mature hedges, indicating a richer concentration of taxa per sample. Irrespective of the measure of diversity used, Mature hedges were superior to New hedges and were significantly richer as well as displaying greater evenness and less dominance. Differences between the hedge types were magnified or minimised depending on the measure used, with evenness measures (Heip and Simpson) in particular highlighting large differences between Mature and New hedges and Hedgeless boundaries. New hedges were marked generally by much larger ranges in values than either Mature hedges or Hedgeless boundaries, the considerable variability suggesting an element of unpredictability or instability in the ecological conditions of these young habitats as they establish themselves.

Values for Coleopteran and Dipteran families showed that taxonomic richness was consistently highest in Mature hedges throughout the months. However, other diversity indices, taking into account relative abundance of taxa, led to different conclusions as to which was the most diverse habitat, depending on month.

It is difficult to find comparable studies from which values of different indices might help contextualise values obtained during this investigation. Shannon is a popular benchmark measure of diversity (Magurran, 2004) so there is more evidence for Shannon than other indices to enable us to take a view on whether the invertebrate diversity levels seen using high level taxonomic analysis bear any relation to diversity levels recorded in farmland boundary habitats.

The significant effect of hedge type on invertebrate diversity at ground level previously reported by Deeming *et al.* (2010), based on 6 farmland hedgerows, was also observed in the larger sample of hedgerows over a wider geographical area. Sticky trapping yielded diversity comparable with that seen for pitfall trapping used by Deeming *et al*. (2010), with mean Shannon *H'* values peaking around 2.0 or just above, but dipping

below 1 for New hedges at their minimum. To give some context to these values, Magurran (2004) indicates that the value of *H'* generally falls between 1.5 and 3.5, rarely surpassing 4. In fact, values seen in this study were comparable with those obtained by Biaggini *et al.* (2007), who reported average *H'* values of <1.0 for Field habitats, ~2.2 for Cultivated Strips and up to ~2.8 for Meadow habitats. Some newly-established hedgerows were therefore similar in diversity to field habitats on this basis, which could reflect at least initial colonisation by a range of taxa broadly adapted to agro-ecosystems, as suggested earlier.

Asteraki *et al.* (2004) studied the effects of different field margin treatments over time on invertebrate diversity, recording 343 species of Coleoptera. However, *H'* diversity values rarely exceeded 2.5 for any of the grass/forb treatments and then only for predator groups of Coleoptera. Values for other phytophagous and detritivorous beetles were lower, ranging from a lowly 0.30 to 2.12 at their highest and rarely exceeding 2.0. In fact, *H'* values averaged for all three functional groups did not exceed 2.0 for any treatment.

The relatively modest peak levels of diversity would therefore seem to be in keeping with what might be expected of 'simplified' or 'impoverished' farmland ecosystems (Biaggini *et al.*, 2007). A broad taxonomic approach appeared to adequately reflect what otherwise work to species level showed – thereby seemingly representing a significant 'short-cut' in assessing diversity at least in agro-ecosystems.

Since hedgerows are a woody habitat, often bracketed with woodland because of the historic origin of some hedgerows as remnant woodland (Pollard *et al.*, 1974), and sometimes treated as 'surrogates' of woodland or at least woodland edges (McCollin *et al.*, 2000), forestry research is relevant. In an American study, Bird *et al.* (2000) examined impacts of forestry practices on the soil and litter arthropod diversity of commercially-managed pine plantations. They used Shannon *H'* as their diversity measure of choice and calculated Shannon *H'* values for their arthropod samples rarely exceeded 2.5 on average, even though they suggested high diversity based on the number of 'morphotypes' found. The morphotype approach embraced a combination of families and orders to characterise the assemblages, and found 43 in total in the samples. Charts depicting the effects of a range of more or less intensive cultivation methods on invertebrate assemblages showed mean *H'* values ranging from well below 1.0 to no more than 2.5. Actual reported values from statistical tests did not exceed 2.0, which puts them in a similar bracket to the values achieved through sticky trapping and taxonomic resolution at order level in this study. Judging by these studies using Shannon *H'*, invertebrate diversity is generally on the low

to intermediate side for agricultural/commercial forestry systems, in keeping with the low taxonomic resolution, although precise relationship with species diversity is unclear.

Experts such as Magurran (2004) appear to mistrust Shannon-Wiener *H*', and Professor Lord Robert May (in the Foreword of Magurran & McGill, 2011) even describes it as 'pernicious' because of the compression of data associated with logarithmic transformation that apparently weakens its discriminatory power. It was however evident from this study that Shannon was equivalent to other measures in its fundamental ability to portray comparative differences between the boundary types using the broad spectrum approach.

4.4.9. The use of broad taxonomic groups to assess diversity at ground level

The task of measuring invertebrate biodiversity in its entirety would be enormous, even in depleted farming ecosystems, hence the continuing drive to develop methods of assessment which would be quicker and cheaper than a whole inventory of species (Duelli & Obrist, 2003; Morrison III *et al*., 2012). Wolton & Vergette (2012) consulted 19 experts on different invertebrate taxa in the course of their inventory of the diversity of life in a single organic hedgerow: this serves as an indication of the enormity of the task in attempting an 'holistic' view of biodiversity, such as that advocated by Wilson (1987). They recorded 1371 species of insect, barring parasitic Hymenoptera, a group which has been estimated to make up about 25% (perhaps more) of the total insect fauna in Britain (Shaw & Hochberg, 2001). The impracticalities of identifying all invertebrates in an ecosystem in this manner, mean that the use of a particular indicator taxon is commonplace, based on an assumption of its ability to behave in ways that represent the rest of the community or assemblage (New, 2005a).

In the farmed environment, a variety of taxa have been used or proposed as shortcuts to characterising insect biodiversity in cultivated and semi-natural habitats, and examples include, *inter alia*: Apoidea (bees) (Billeter *et al*., 2008); Araneae (Billeter *et al*., 2008); Carabid or Staphylinid beetles (Holland *et al*., 2002; Biaggini *et al*, 2007; Billeter *et al*., 2008); Syrphidae (Diptera: hoverflies) (Sommaggio, 1999; Dziock & Sarthou, 2005; Billeter *et al*., 2008); Heteroptera (bugs) (Billeter *et al*., 2008); parasitoid Hymenoptera (Anderson *et al.*, 2011). Combinations of taxa are also recommended as substitutes for invertebrate diversity, with some overlap but overall no consensus, *e.g.* Hemiptera and Coleoptera (Morrison III *et al.*, 2012); Auchenorrhyncha (leafhoppers and their relatives), Heteroptera (bugs), Araneae and Coleoptera (Asteraki *et al.*, 2004); Heteroptera, Symphyta

(sawflies) and aculeate Hymenoptera (bees and wasps) (Duelli & Obrist, 1998). However, the use of a single indicator taxon approach ignores the unpredictability or even lack of relationship between the diversity of different groups (Prendergast, 1997; Duelli & Obrist, 2003; Billeter *et al.*, 2008; Gerlach *et al.*, 2013).

Anderson *et al.* (2011) have shown that the *abundance* of parasitoid Hymenoptera (crucially, not the speciosity, which is very high, nor even the diversity at family level which the authors acknowledge would require considerable expertise) is a good correlate with wider arthropod diversity in agro-ecosystems and a feasible option for simple, practical monitoring of change. Evidence for the suitability of Hymenoptera Parasitica as a stand-alone bioindicator was based on their correspondence with 4 other invertebrate taxa, *i.e.* Araneae, Coleoptera, Diptera and Hemiptera, and the relationship with the wide range of other groups was not tested. Some taxa will be poorly represented by an indicator.

This study found that Hymenoptera (including Formicidae and Aculeates) were the 'best' overall correlate with other taxa in terms of abundance, being correlated with 11 other taxa at ground level. Nonetheless, there were two taxa whose numbers bore no relationship with Hymenoptera, nor any other taxon: Julida and Psocoptera. In addition, the abundance of Hymenoptera was also found to be correlated with taxon richness (for all months combined) but no other diversity measure. An analysis of the Parasitica separately showed them to be a better correlate with diversity measures, although other taxa had stronger correlations with diversity. The suggested use of Hemiptera (Morrison III *et al.*, 2012) is interesting in relation to this study, since abundance of Hemiptera showed significant relationships with most measures of diversity, perhaps reflecting their position as a significant mixed group of herbivores, hosts and predators in agro-ecosystems. However, Opiliones were the 'best' positive correlate with all diversity measures. The reasons for this are unclear, but reflect an association between the increase in harvestman numbers and an increase in evenness and richness in the assemblage.

Conducted to identify possible 'indicators' or predictors of boundary types, decision tree analysis identified different taxa as having the best discriminatory function depending on month of sampling – Thysanoptera provided the best split between Mature and New hedges, but then only in July. It was also evident in my study that there was no single overarching good surrogate group which would accurately represent overall diversity at ground level, although there were several which, depending also on the time of year, correlated well with a number of other taxa in terms of abundance. My results therefore underlined how difficult it would be to extrapolate the condition of invertebrate

populations in different habitats from just one taxon or 'bioindicator'. Also, the different responses of invertebrate taxa to time of sampling as well as boundary type, suggest that a single indicator taxon would be unsuited to reflecting the seasonal patterns of invertebrate abundance and diversity in hedge bottoms. Although single taxa can be relevant and sensitive indicators of particular processes, broader groups have the advantage that compositional features can also be evaluated and perhaps mirror a wider variety of conditions (New, 2005a).

As such, an order-level approach, proposed by Biaggini *et al.* (2007) and used in this study, also takes in essence a 'bioindicator' role – anything other than a full inventory of species inevitably will - and may well be a 'simplification of what probably happens in nature' but cannot be dismissed as trivial (Paoletti, 1999). In this study, it achieved the purpose of being able to make a comparison between the respective diversities of hedgerow/hedge-free habitats. The superior diversity of Mature hedges at least at ground level was apparent, although the extent to which New hedges lagged behind less so.

4.4.10. Sticky trapping as a method

Sampling methodology can affect the perception of rarity (Longino *et al*., 2002, cited by Magurran, 2004) and this is discussed above with relation to apparently rare taxa such as Neuroptera and whether this indicates true sparsity. Sticky traps were seen to be capable of sampling a wide range of taxa, but sampled some taxa more effectively than others and a number of taxa were very scarce in the samples. Some of this bias was undoubtedly a consequence of preventing by-catch with use of wire mesh. However, as discussed above, in some cases, this might be because of genuinely low densities of certain organisms in the farmed environment and/or it may be that sticky trapping is not the optimal method of trapping those organisms. It is highly unlikely however that any single method could sample all taxa equally efficiently (New, 1998). Even pitfall trapping, although extensively used and relied upon as a means of collecting large numbers and a wide diversity of invertebrates at ground level is not a comprehensive sampling method (New, 1998; Southwood & Henderson, 2000). The inability of sticky traps to be a 'catch-all', therefore, does not matter too much given that self-evidently any particular method for collecting invertebrates will be selective to some extent (Disney *et al.*, 1982, cited by New, 1998; Gullan & Cranston, 2005). The purpose here was to make a comparative assessment of biodiversity between habitats rather than inventory and the method was replicated throughout the habitats sampled. Furthermore, the traps did serve the purpose of sampling

invertebrates from a range of different groups. Diehl *et al.* (2013) indicated that, in addition to Hemipterans, Dipterans, Hymenopterans, and Thysanopterans were well-represented on sticky traps, which was also the case in this study. Analysis of Coleopteran and Dipteran families shows that groups found in other research to be dominant in agro-ecosystems were also generally the largest groups caught on sticky traps (Carabidae, Chrysomelidae, Lathridiidae Staphylinidae, Phoridae and Nematocerans, notably Sciaroidea).

The precursor to this study (Deeming *et al*., 2010), had employed pitfall traps, another passive sampling method, which was also not assumed to be capable of trapping every taxon equally effectively, but adequate for the purposes of making a comparison of habitats as opposed to an inventory. Although there were some similarities between the composition of invertebrate samples from sticky traps and those from pitfall trapping, there were also differences. Gullan & Cranston (2005) indicate that pitfall catches may be dominated by a few taxa, notably Collembola and Hymenoptera (in particular Formicidae), and Coleoptera (notably Carabidae, Staphylinidae, Tenebrionidae and Scarabaeidae). This also holds true to an extent for sticky trap catches, *i.e.* Collembola and Hymenoptera tended to dominate, although Collembola were less dominant in sticky traps than in pitfall traps. Coleoptera were also numerically a far less dominant element of sticky trap samples than found in previous work using pitfall traps. By contrast, Acari were, for example, a much more dominant element of sticky trap catches than of pitfall catches. For some taxa, *e.g.* Araneae, there appeared to be little difference between the two trapping methods in the average numbers caught per hedgerow/boundary. Preliminary work conducted in 2010 as a 'pilot' to the present study provided a direct comparison between the trap types and indicated that pitfall traps were capable of collecting significantly greater numbers of invertebrates than sticky traps, but also corroborated the observation from Deeming *et al.* (2010) data that sticky trapping samples a different 'fraction' of invertebrate diversity from pitfall traps.

The number of apparently rare taxa on sticky traps might be an indication of its lack of effectiveness for certain groups, but also a reflection of genuine lack of abundance at ground level for others. For some taxa, sampling effect may have been less important in influencing numbers of organisms than thinly distributed populations. Lepidoptera were, for instance, seldom caught, but this was thought to be not necessarily an artefact of the trap type used, but rather a reflection of sparsity in the farmed environment for butterflies (Defra, 2012) and suboptimality of hedgerows as moth habitat (Fuentes-Montemayor,

2011a, 2011b). Thanks to the status of butterflies as a national biodiversity indicator a great deal is known about their population trends in recent times. The conspicuous decline of farmland butterfly populations has taken place during the course of the three decades, overlapping with the existence of AES. Lepidoptera on University of Lincoln farmland were also deemed scarce using visual transect and water trap techniques, according to unpublished data from other hedgerow biodiversity investigations (Farrow, 2011, unpublished dissertation).

Neuroptera were also seldom caught in sticky traps. For catching Neuroptera at ground level Plant (1997) recommends pitfall traps, water traps, direct searching and suction sampling. Reportedly, lacewings can be as abundant as Carabid and Staphylinid beetles in grasslands when using a suction sampler (Plant, 1997). No Neuroptera were caught during a year of pitfall trapping in farmland hedgerows (Deeming *et al.*, 2010), nor during an 11-week survey of winged insects using direct searching and water traps in the same habitat (Farrow, 2011, unpublished). Neuroptera might be genuinely low in density and only sporadically found in farmland hedges, at least at the Lincolnshire sites used. A focal study of these organisms using, for instance, an active sampling method such as suction in tandem with alternatives such as sticky traps would help rule out sampling effect.

Obtaining comprehensive samples representative of diverse assemblages is challenging, particularly if only one sampling technique is chosen, and there is a strong element of change in some captures (New, 1998). Use of a number of different trapping techniques to maximise the possibility of detecting the presence of perhaps abundant but hard to trap species is desirable, but has its own issues and if the objective is a comparative view of ecosystems rather than an absolute inventory of numbers or taxa then one trapping technique used consistently should be adequate. Sticky trapping as a stand-alone technique was found to be suitable for collecting large numbers of a range of invertebrate taxa on which an assessment of diversity in the hedge bottoms/hedgeless boundaries could be based. The fact that some taxa were trapped less effectively than others should not matter where the same trap type was replicated: catches can be deemed comparative.

4.4.11. Conclusion

Differences between the boundary types were manifested at the taxonomic level of Order, but evidence was mixed for the effect of age on the abundance and diversity of individual invertebrate taxa collected from the hedge bottoms. Contrary to expectation,

Mature hedges did not appear important to invertebrate abundance at ground level/in the hedge bottom. In fact, the presence of a hedgerow *per se* did not seem to be a prerequisite for invertebrate abundance. This fits with the findings of Pywell *et al.* (2005), who found no significant effect of hedge age on overall abundance of epigeal Araneae and Coleoptera, attributing this to good dispersal ability, but also to the close relationship between habitat age and characteristics such as botanic composition and structure. Pywell *et al.* (2005) indicated that the effect of habitat age can be "masked" by the influence of habitat characteristics, since composition and structure change with time and management. Indeed, this study also indicated that a mature hedge is associated with a particular set of conditions on the ground and the invertebrate fauna it supports are a reflection of those conditions rather than maturity *per se*, albeit that growth form and the ageing process would seem to have a strong influence.

Although a difference was shown between boundary types in terms of invertebrate diversity, and Mature hedges exhibited generally higher diversity values than New hedges at ground level, hedge maturity explained only a proportion of the variability in the composition of invertebrate assemblages in this investigation. Just as Pywell *et al.* (2005) identified a few taxa which responded to mature boundary habitats, a small selection of taxonomic groups were more abundant in Mature hedges (notably certain detritivorous taxa), or showed a significant correlation with hedgerow age, including Coleoptera and Diptera. The fact that these large, speciose, multi-functional groups responded well might indicate the increase in a range of suitable ecological niches over time, fitting the initial hypothesis of an effect of maturity on diversity. Hedgeless boundaries apparently supported higher populations of certain taxa (Araneae and Hemiptera). This indicates that although the presence of a hedge tends to benefit a range of invertebrates, there are some important taxa, including beneficial predators, which may not be best supported by the planting of hedgerows. Nonetheless, although the new-planting of hedgerows under AES might not be optimal for maintenance, restoration or enhancement of all components of the invertebrate assemblage, it appears to represent a relatively quick, though modest, gain for invertebrate biodiversity at ground level.

The conditions of the woody hedge 'canopy' and the effects of other variables on invertebrate abundance and diversity are described and discussed in further detail in Chapters 5 and 6. Key points and conclusions are summarised in Chapter 7.

Chapter 5. Effects of hedge age on invertebrate assemblages of the canopy

5.1. Introduction

In comparison with the body of research investigating ground level conditions of farmland hedgerows at hedge bottom/base, there are relatively few examples of published research examining the invertebrate assemblages of hedgerow canopies (*i.e.* the woody hedge itself). An inventory of hedgerow invertebrates on one historic hedgerow (Judith's hedge) was conducted by Pollard *et al.* (1974), and one or two more recent studies have focused on the fauna of the woody as opposed to the grassy element of farmland hedgerows (notably Joyce et al., 1997; Maudsley *et al.*, 1997, 2002; Pollard & Holland, 2006). Both Maudsley (2000) and Barr *et al*. (2005) produced reviews suggesting that the invertebrate fauna of the woody part of hedgerows was still poorly understood. There are nonetheless still few studies examining the current state of invertebrate assemblages in the UK's hedgerows. Hence evidence for the benefits of hedgerows to invertebrates in the UK is lacking (Boatman *et al.*, 2008), particularly regarding the effectiveness of AES options where the need is arguably greatest. Although there is some evidence that work has been done to address this deficit, *e.g.* for Lepidoptera (Mercx *et al*., 2012) and functional communities (Amy *et al*., 2015), and there are continuing deficits in information for certain groups, particularly regarding those taxa which have no obvious agro-ecosystem service role in pest control or pollination, or as umbrella/flagship species (Staley *et al.*, 2012b).

The Hedgerow Futures conference (September 2012) corroborated the impression that after something of a heyday of hedgerow related research in the late 1990s and early 2000s which helped inform agri-environmental policy and practice, there appears to have been a decrease in research activity relating to hedgerow invertebrates. Wolton and Vergette (2012) plugged some gaps in contemporary knowledge by conducting an entire inventory of hedgerow invertebrates, but based on a single hedgerow on an organic livestock farm in Devon. This may not bear comparison with hedgerows of a conventionally farmed arable landscape such as large parts of Lincolnshire.

When measuring invertebrate diversity in agricultural ecosystems, researchers have tended to focus their attention on one or two groups. For instance, Lepidoptera (butterflies and moths) is a relatively well-studied, so-called 'charismatic' (Fleishman & Murphy, 2009) taxon which has been used to evaluate how invertebrates in general have benefited

from AES. The assumption is that any gains seen for Lepidoptera are transferable to other taxa and that members of this group can therefore act as "bioindicators of landscape-scale quality", presumably for invertebrates as a whole (Merckx *et al*., 2009). Farmland butterflies are the UK government's primary insect/invertebrate biodiversity indicator because, it is claimed, they are "representative of many other insects" (Defra, 2012). Likewise, the invertebrate diversity of the woody elements of farmland hedgerows has been measured using 'proxy' taxa, such as Heteroptera (Hemiptera) (Maudsley *et al.*, 1997). Maudsley *et al.* (2002) used selected invertebrate taxa (Carabid and Staphylinid beetles and Araneae) to assess the quality of woody hedgerow habitat for predatory arthropods in general. The vast number of less familiar and less charismatic species can not only present identification issues (in terms of expertise, time and money available), but are also probably of less concern to the agriculturalist than potentially economically important pests/predators. Consideration of such functional groupings is desirable to the farming community and is therefore a widespread approach in investigations of invertebrates in agro-systems. This is another reason broad spectrum studies of hedgerow invertebrates are uncommon in the literature. Since sustaining biodiversity *per se* has become a widely recognised goal for AES and for hedgerows (Baudry & Bunce, 2001), a broader non-functional view seems justified.

New hedges planted under AES have been added to the landscape under the presumption that they have a role in sustaining a diversity of organisms. An important question is whether adding hedgerows to the farmed environment has had a beneficial effect on the abundance and/or diversity of hedgerow invertebrates. Is it possible to say whether hedgerow planting has been money well-spent in this respect? Since agri-environment scheme funds for planting new hedgerows ceased in large part in the mid-2000s, monies have been refocused more on management, and there has been recent interest in how management prescriptions work to benefit hedgerow fauna. Staley *et al*. (2012a) have, for instance, suggested alterations to policy, advice and practice of hedgerow cutting, which might benefit some invertebrates. Sam Amy (personal communication) of the Centre for Ecology and Hydrology is conducting research into the effect of management on the invertebrate fauna of farmland hedgerows. But to my knowledge, no studies expressly address the question of invertebrate diversity in the woody parts of new plantings under agri-environment schemes (AES).

Just as the ground-level invertebrate assemblage of newly-planted hedges was described in Chapter 4, this chapter compares the canopy-active invertebrate assemblages

of mature versus more recently established hedgerow habitats. As before a broad taxonomic approach was taken to investigate the effect of age on the abundance and diversity of invertebrate fauna of the hedge top.

5.2. Methods

An adapted beating method was selected to target invertebrates of the 'canopy' of hedgerows. Beating entails tapping and shaking off small animals by striking aerial vegetation, such as hedgerow canopies. It is recognised in ecological literature as a method of collecting individual specimens and in assessing and estimating invertebrate populations of tall vegetation and woody habitats (*e.g.* New, 1998; Southwood & Henderson, 2000; Drake *et al.*, 2007). The technique is not widely employed to sample whole communities, although there are examples of the use of beating/jarring to collect broader samples, *e.g.* Southwood *et al*. (1979). Amy *et al.* (2015) used a beating technique to investigate the effects of rejuvenation treatments on the invertebrate diversity of hedge canopies.

Beating is simple and cheap and the equipment easily portable. It is capable of large catches, including mobile species, although this is dependent on type and structure of habitat and there is the risk of an 'escapee' component, which varies amongst taxa (New, 1998). Beating is also weather-dependent and cannot be used if vegetation is wet; it is also best avoided in windy conditions. In common with the majority of sampling methods, both terrestrial and aerial, the beating technique may only be expected to provide at best an indicative partial representation of the diversity of invertebrates living in a canopy habitat.

The adapted method used in this study entailed 'beating' or rather tapping hedgerow vegetation at the lower canopy level – ~1m from the ground – at 8 equidistant points along the central 30 m length of hedgerows to dislodge invertebrates into a collecting container via a large wide-necked plastic funnel, widened with the use of an 'Elizabethan' dog collar to a diameter of 50cm (see Chapter 3, Figs. 3.8 & 3.9). The collecting beaker contained a paper towel substrate for the invertebrates to land on and a piece of cloth impregnated with a small quantity of the killing agent ethyl acetate. Cloth covers were used to 'seal' the collecting beakers and prevent sweating of the samples which were placed in a cool bag during the survey work. Samples were subsequently frozen to ensure sampled organisms had been killed and for preservation prior to identification.

Invertebrates were identified using a zoom dissection microscope (capable of up to x90 magnification) and sorted into taxa, focusing on Order level, or sub-Class in the case

of Acari (ticks and mites), in accordance with Tilling's (1987) 'major groupings'. The diversity of samples was measured in the same way as sticky trap samples in Chapter 4, using taxon richness (number of different 'major groupings') and widely used and simple-to-calculate diversity indices, including Shannon and Simpson (Magurran, 2004). Descriptive and analytical statistical techniques are as described in the General Methodology (Chapter 3), and as used for reporting sticky trapping results (Chapter 4).

5.3. Results

5.3.1. Abundance of hedge canopy invertebrates and their taxonomic groupings

A total of 11,665 organisms from 17 invertebrate taxa (Order/Class) were collected from the canopies of two types of hedge, 'Mature' and 'New', using a beating technique. Greater numbers of invertebrates were collected in all from Mature hedges (6,194) than from New hedges (5,471), although the monthly averages produced a very similar pattern irrespective of hedge age (Fig. 5.1). There was substantial variation in numbers caught in individual hedgerows, ranging from single figures, from a New hedge in April, to a peak of more than 600, from a Mature hedge in July. GLM indicated no significant effect of hedge type as a main effect and no significant interaction with month of sampling (Table 5.1). The effect of month of sampling was significant, with July by a clear margin the month of highest abundance in both hedge types (Fig. 5.1): over twice as many organisms were collected in July as in either April or September (Appendix C, Table C1).

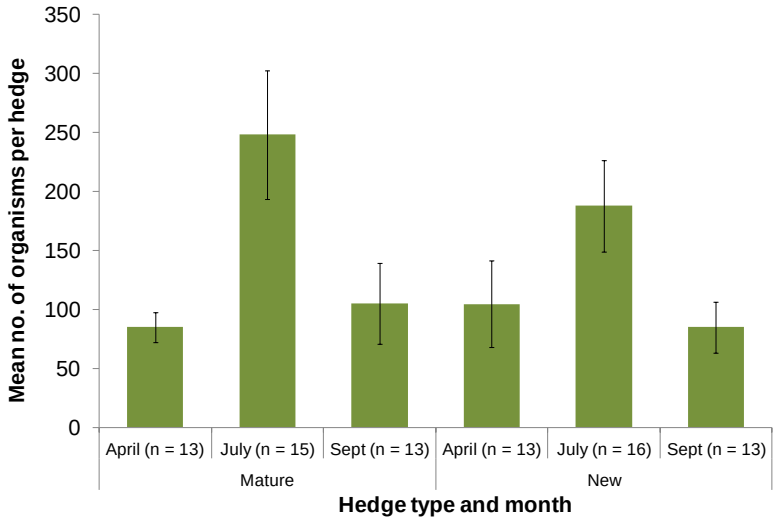


Figure 5.1. Mean abundance (± SE) of all taxa collected by beating, per boundary type (Mature hedges and New hedges) per month (April, July, September) in 2011

Table 5.1. Results of a Generalised Linear Model analysis of the effects of month (April, July, September) and hedge type (Mature hedges, New hedges) on the total abundance of all invertebrate taxa

All Taxa	Effect					
	Month		Boundary type		Interaction Month* Boundary type	
	Wald χ^2	*p*	Wald χ^2	*p*	Wald χ^2	*p*
Total abundance	13.143	0.001	0.183	0.669	0.938	0.626
	12.934	**0.002**	0.232	0.630	Main effects only	

Taxonomic Abundance Distributions (TADs) of the canopy-active invertebrates are shown in Figure 5.2. These TADs, at least for April and July, show approximations of a 'hollow' (concave) curve for both hedge types, in keeping with the classic shape of a Species Abundance Distribution (SAD) on which they are based. The 'curves' indicate few very abundant taxa and a relatively large number of moderately abundant or even 'rare' or infrequently sampled taxa. Visually there would seem to be little to choose between Mature and New hedges. Indeed, in April and July analysis by ranked ANCOVA indicated there was no significant difference between the TAD curves (Fig. 5.2a & b). A statistically significant difference between the ranked taxonomic distributions of the Mature and New hedge types was however found in September (Table 5.2); Mature hedges were showed significantly higher abundance distributed across a larger number of taxa than New hedges with clearer separation between distribution curves (Fig. 5.2c).

TADs do not directly identify taxa, and so to further aid visualisation of patterns in the count data from beating, the following section provides an overview of average canopy-active invertebrate abundance for each named taxon, month and hedge type. Additionally, the taxa have been 'ranked' according to abundance (Table 5.3). Highly abundant taxa such as Collembola, comprise thousands of individuals in total, contrasting with the very 'rare' taxa that numbered only one or two individuals. This is a similar pattern to that seen for invertebrates sticky-trapped at ground level, with numbers collected from the canopy being overall considerably fewer.

Only Mature hedges yielded specimens of all 17 taxa, and then only in July (Appendix C, Table C2). New hedges yielded 15 taxa in total for all months combined, although there were some differences between months, notably in April, when the number of taxa in New hedges (14) exceeded that in Mature hedges (12), but not significantly so.

Mature hedges generally had a lower proportion of 'rarities' (≤1 specimen per hedge). There was however little to choose between the two hedge types, confirmed by analysis of individual taxa below, which showed some variation, both in terms of seasonal variation and differences between hedge ages.

5.3.2. Effect of hedge type and month on invertebrate abundance at canopy level

Broad patterns of abundance suggested the influence of both hedge type (Mature/New) and month on distributions of different canopy-active invertebrates. Isopoda, Julida, Neuroptera and Polyxenida were not tested due to their very low abundance.

No significant interaction between month of sampling and hedge type was found for any taxon, although for three (Acari, Coleoptera, and Hymenoptera) the interaction approached statistical significance. Month had a significant effect on abundances of the majority of taxa (Table 5.4). There was however a statistically significant difference between numbers found in Mature hedges compared with New hedges for four taxa only: Acari, Hemiptera, Lepidoptera and Pulmonata. That month was significant in determining the overall abundance of invertebrates (Table 5.1) reflects the fact that month rather than hedge type was the decisive influence on invertebrate numbers for the majority of individual taxa (Table 5.4; Appendix C, Table C2).

The following section describes in greater detail patterns of distribution across boundaries and months following an order from most to least abundant organisms overall, as indicated in the ranking in Table 5.3. Column charts have been generated for each taxon to highlight the differences and/or similarities between mean counts (±SE) in different boundary habitats and months (Fig 5.3a-m). Further supporting data, showing detailed month-by-month count data (including means, ±SD and ±SE) for each taxon and boundary type, has been tabulated and can be found in (Appendix C, Tables C3 – C5).

Collembola were by a considerable margin the most abundant taxon collected from the canopy overall and were the top ranked taxon in all months (Table 5.3). Mean counts of Collembola showed a similar pattern for both Mature and New hedges across the months, peaking in July at similar levels with similarly wide variation about the mean (Fig. 5.3a). Although numbers were higher in New hedges in April, GLM (Table 5.4) indicated no statistically significant effect of hedge type although a highly significant effect of month was shown.

Coleoptera ranked second in terms of overall abundance (Table 5.3) and were a relatively more important component of the invertebrate assemblage of the canopy than

they had been at ground level. Numbers were unevenly distributed throughout the months with Mature hedges showing a different pattern to New hedges (Fig. 5.3b). April was the peak month for Mature hedges and July for New hedges. Catches of Coleoptera in New hedges in September were markedly lower than at any other time (Fig. 5.3b). In total numbers were marginally greater in New hedges (Appendix C, Tables C3-C5). GLM did not show a significant effect of hedge type, although there was a significant difference between monthly distributions (Table. 5.4).

Investigation of the Coleopteran samples at family/superfamily level, indicated that there was a large amount of overlap in groups represented in the two hedge age groups. There was no significant difference between numbers of respective underlying families/superfamilies for all months combined (Mann-Whitney U = 604.50, p = 0.925). Latridiidae (minute scavenger beetles), Curculionoidea (weevils), Chrysomelidae (leaf beetles) and Coccinellidae (ladybirds) were the largest groups of both hedge types across the months (Appendix C, Tables C6-C8). In total, Coccinellidae and Curculionidoidea were more abundant in New hedges, and Latridiidae in Mature hedges. Latridiidae was most abundant in April and also collected in relatively large numbers in July and September from both Mature and New hedges. Chrysomelidae were also comparatively common during in April, particularly in Mature hedges, but not in other months. Other groups were collected in much lower numbers, including groups more commonly associated with the ground such as Carabidae and Staphylinidae (Appendix C, Tables C6-C8). Considerably fewer families were present in catches from the hedge top than at ground level:17 versus 36 (Appendix B, Tables B8-B10).

Hemiptera were the third most abundant group overall in samples from the canopies of both hedge types (Table 5.3), but were particularly numerous in July (Fig. 5.3c; Appendix C, Tables C2-C5). More specimens were caught for each month from the hedge tops of Mature hedges than of New hedges. The contrast in abundance was most conspicuous in July, albeit with considerable variability about the mean (Fig. 5.3c). Reflecting this pattern, the GLM showed a significant effect of hedge age type and a highly significant effect of month (Table 5.4).

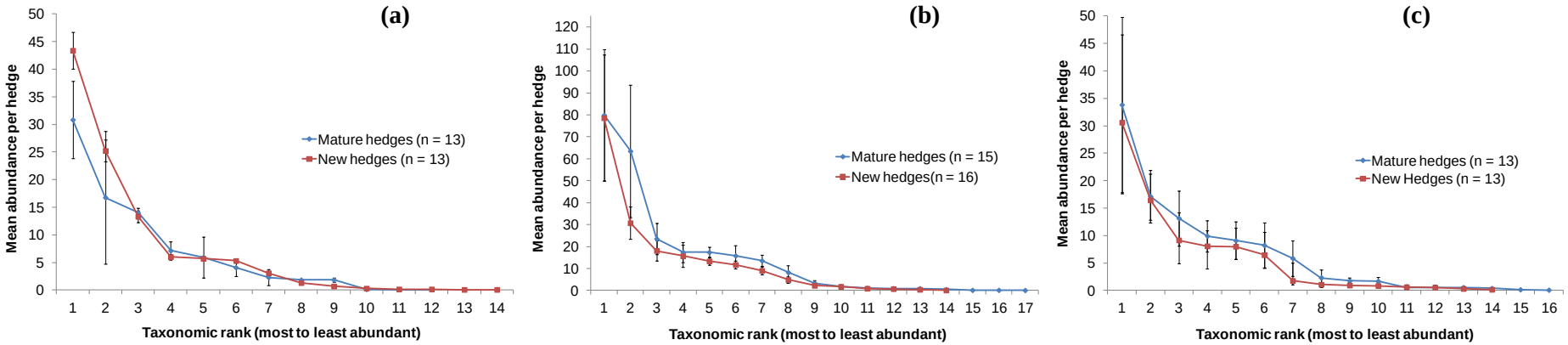


Figure 5.2a-c. Taxonomic Abundance Distribution curves for canopy-active invertebrates collected in: (a) April; (b) July; (c) September. Line plots show mean number of organisms (+/- SE) per hedge against taxonomic rank (most to least abundant) for both Mature and New hedges

Table 5.2. Results of a ranked ANCOVA (Quade procedure*) comparing taxonomic abundance distributions (TADs) of Mature hedges and New hedges for each month of sampling (April, July and September)

	Quade ANCOVA			Comparisons of residual values	
Month	**df**	**F**	***p***	**Mature mean**	**New mean**
April	1,24	1.912	0.179	-0.322	0.276
July	1,29	3.160	0.086	0.398	-0.483
September	**1,28**	**28.629**	**<0.001**	0.956	-1.093

* **The Quade (1967) procedure is described in Chapter 3, section 3.12.1.**

Table 5.3. Taxonomic rank showing total abundance of canopy invertebrates for individual taxa ranked from most to least abundant. Totals for each month (April, July, September) and a grand total for All months and both boundary types (Mature hedges and New hedges) combined

Rank	Total abundance, all boundaries summed							
	All months (n = 83)		April (n = 26)		July (n = 31)		September (n = 26)	
	Taxon	Total	Taxon	Total	Taxon	Total	Taxon	Total
1	Collembola	4075	Collembola	782	Collembola	2455	Collembola	838
2	Coleoptera	1808	Coleoptera	729	Hemiptera	1241	Araneae	385
3	Hemiptera	1646	Araneae	250	Coleoptera	752	Coleoptera	327
4	Araneae	1109	Acari	222	Acari	604	Hemiptera	234
5	Acari	916	Hemiptera	171	Araneae	474	Hymenoptera	226
6	Hymenoptera	706	Diptera	127	Thysanoptera	390	Psocoptera	202
7	Thysanoptera	445	Hymenoptera	99	Hymenoptera	381	Acari	90
8	Psocoptera	405	Thysanoptera	41	Psocoptera	200	Diptera	53
9	Diptera	258	Lepidoptera	33	Diptera	78	Opiliones	35
10	Lepidoptera	85	Dermaptera	6	Pulmonata	51	Dermaptera	30
11	Pulmonata	69	Psocoptera	3	Lepidoptera	41	Pulmonata	16
12	Dermaptera	61	Pulmonata	2	Dermaptera	25	Thysanoptera	14
13	Opiliones	55	Neuroptera	2	Opiliones	19	Lepidoptera	11
14	Neuroptera	12	Opiliones	1	Neuroptera	7	Julida	7
15	Julida	8	Polyxenida	0	Isopoda	3	Neuroptera	3
16	Isopoda	5	Isopoda	0	Polyxenida	2	Isopoda	2
17	Polyxenida	2	Julida	0	Julida	1	Polyxenida	0
	Grand Total	**11,665**	**Total April**	**2,468**	**Total July**	**6,724**	**Total Sept**	**2,473**

Table 5.4. Results of a Generalised Linear Model (GLM) analysis of the abundance of all invertebrate taxa collected through beating from the hedge canopies. The effect of time (Month: April, July, September) and habitat (Mature hedges versus New hedges) is compared. Values are Wald χ^2 plus significance values. Significant values are highlighted in bold

Taxon	Month		Hedge type		Interaction Month*Hedge Type	
	Wald χ^2	*p*	Wald χ^2	*p*	Wald χ^2	*p*
Acari (Fig. 5.3e)	45.927	<0.001	23.354	<0.001	5.941	0.051
	44.199	**<0.001**	**19.221**	**<0.001**	Without interaction	
Araneae (Fig. 5.3d)	4.445	0.108	1.236	0.266	3.741	0.154
	3.797	0.15	0.841	0.359	Without interaction	
Coleoptera (Fig. 5.3b)	10.212	0.006	0.34	0.56	5.971	0.051
	9.135	**0.010**	0.134	0.715	Without interaction	
Collembola (Fig. 5.3a)	18.958	<0.001	1.546	0.214	4.379	0.112
	17.374	**<0.001**	1.207	0.272	Without interaction	
Dermaptera* (Fig. 5.3l)	7.987	0.018	0.256	0.613	2.49	0.288
	8.721	**0.013**	1.528	0.216	Without interaction	
Diptera (Fig. 5.3i)	8.513	0.014	0.552	0.458	2.615	0.271
	8.81	**0.012**	0.544	0.461	Without interaction	
Hemiptera (Fig. 5.3c)	40.993	<0.001	5.567	0.018	5.145	0.075
	40.825	**<0.001**	**6.700**	**0.010**	Without interaction	
Hymenoptera (Fig. 5.3f)	18.118	<0.001	0.276	0.599	5.732	0.057
	16.3	**<0.001**	0.03	0.864	Without interaction	
Lepidoptera (Fig. 5.3j)	6.94	0.031	4.689	0.03	0.235	0.889
	7.499	**0.024**	**5.675**	**0.017**	Without interaction	
Opiliones (Fig. 5.3m)**	Some convergence criteria not met. Validity of model fit uncertain.					
	13.396	**0.001**	2.614	0.106	Without interaction	
Psocoptera (Fig. 5.3h)	40.159	<0.001	0.016	0.898	0.86	0.651
	43.159	**<0.001**	1.951	0.162	Without interaction	
Pulmonata* (Fig. 5.3k)**	Some convergence criteria not met. Validity of model fit uncertain.					
	18.992	**0.001**	**4.865**	**0.027**	Without interaction	
Thysanoptera (Fig. 5.3g)	88.3	<0.001	290	0.59	0.189	0.90
	88.103	**<0.001**	0.434	0.51	Without interaction	

*On testing for main effects, GLM gave warning that maximum no. of step-halvings reached but log likelihood value could not be improved. Output for last iteration displayed. Validity of model fit uncertain

**No Opiliones for Mature hedges in April and only one for New hedges

***No Pulmonata for Mature hedges in April and only 2 counts for New

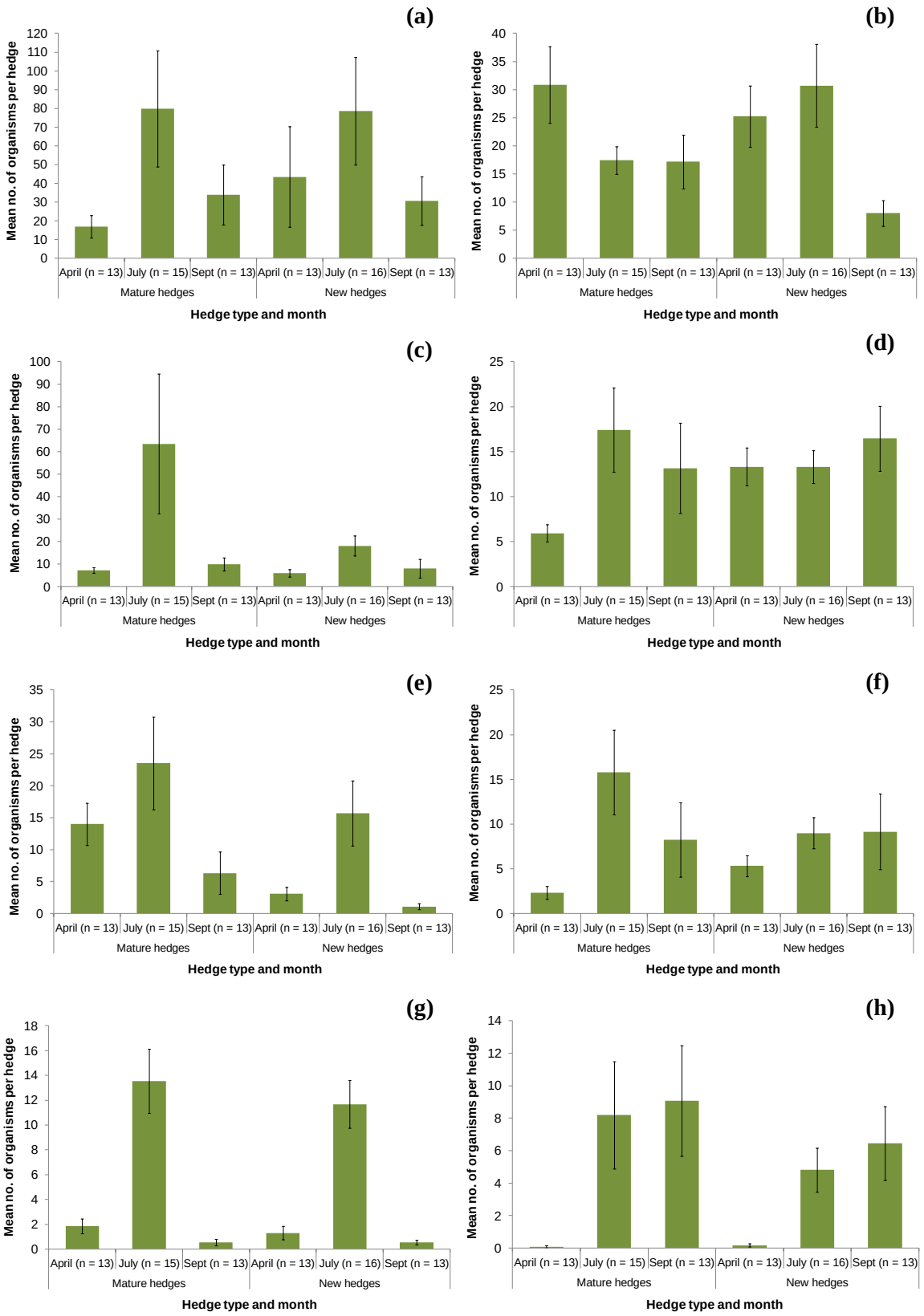


Figure 5.3a-h. Mean abundance (± SE) of taxa collected by beating, per boundary type (Mature hedges and New hedges) per month (April, July, September) in 2011: (a) Collembola; (b) Coleoptera; (c) Hemiptera; (d) Araneae; (e) Acari; (f) Hymenoptera; (g) Thysanoptera; (h) Psocoptera

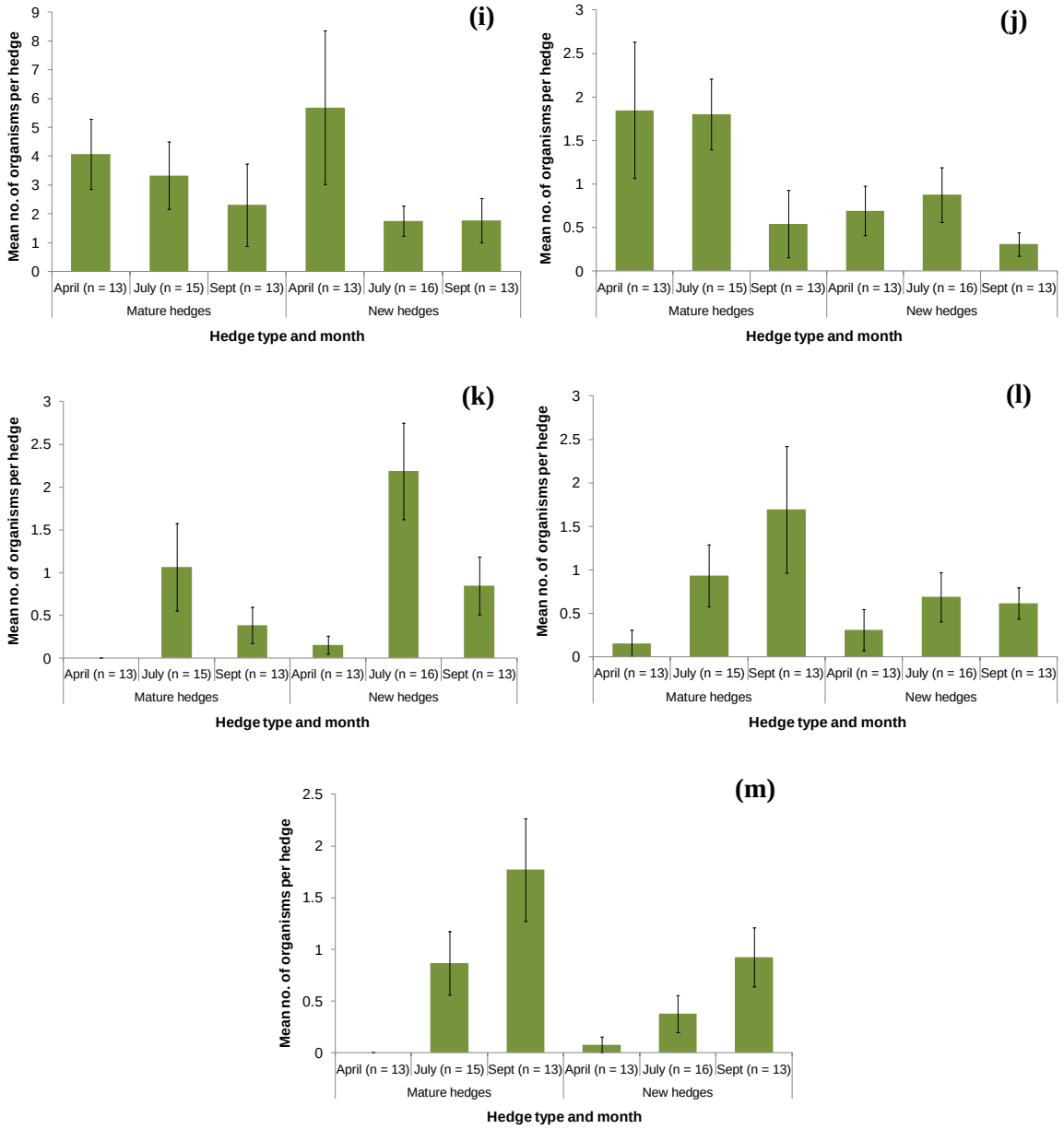


Figure 5.3i-m. Mean abundance (± SE) of taxa collected by beating, per boundary type (Mature hedges and New hedges) per month (April, July, September) in 2011: (i) Diptera; (j) Lepidoptera; (k) Pulmonata; (l) Dermaptera; (m) Opiliones

Psyllids and Aphids tended to account for a large portion of the Hemipteran fauna and comprised over 50% of the total assemblage for all months and both hedge types. Heteropterans such as Anthocoridae (flower/pirate bugs), Miridae, Pentatomoidea (shield bugs) and Tingidae (lace bugs), as well as Cicadomorpha (leafhoppers, froghoppers *etc*.) were also well-represented in the rest of the assemblage, although much fewer than Aphids/Psyllids. In so far as they could be identified, Hemipteran assemblages appeared similar irrespective of hedge age, although Psyllids were more dominant in Mature hedges and Aphids in New hedges. Tingidae were always more numerous in samples from Mature

hedges compared with New hedges (53 versus 17 in total). Scale insects (Hemiptera: Coccoidea) were found in small numbers and only in Mature hedges.

Araneae were in the top 5 most abundant groups sampled from the canopies, with >1,000 sampled in total (Table 5.3). More Araneae were collected in total from the canopies of New hedges than from Mature hedges and July was the month of highest mean abundance in Mature hedges whereas numbers were highest in September in New hedges (Fig. 5.3d). Overall these differences were, however, very small and Araneae showed neither a statistically significant effect of hedge type, nor of month (Table 5.4).

There was a highly significant effect of hedge type was shown on numbers of Acari at canopy level (Table 5.4). Numbers of Acari were conspicuously higher in every month in Mature hedges (Fig. 5.3e). A highly significant effect of month was also indicated by the GLM and this reflected the clear difference between numbers in July compared with other times of the year for both boundary types, although more dramatically in New hedges.

Hymenoptera were present in good numbers in the canopy and differences between numbers of Hymenoptera in Mature and New hedges, particularly in July, are highlighted in Figure 5.3f. Although there was a highly significant effect of month on Hymenopteran abundance, there was no indication of a statistically significant effect of hedge type (Table 5.4).

Below the level of order, further classification revealed that Hymenoptera Parasitica (including Chalcidoidea, Ichneumonids and Cynipidae) accounted for the vast majority (>80% overall) of Hymenopterans collected from hedge canopies using the beating technique, with other groups such as larval forms of Symphyta (sawflies) present in much smaller numbers (Appendix C, Figs. C1 a-c). Formicidae (ants) were found in small numbers in the hedge canopy. Hymenoptera appeared to be well dispersed amongst hedgerows and there was no absolute dominance of one hedgerow, nor one hedge age group (Mann-Whitney $U = 145.00$, $p = 0.485$). Only two wasps (Vespidae) were collected during the entire sampling regime and no specimens of bees (Apidoidea) were collected using this technique.

Thysanoptera were collected in greater number from Mature hedges, but differences between the two hedge types were effectively minimal and there was a very similar monthly pattern, with a spike in abundance in July in both (Fig. 5.3g). There was no significant difference between numbers of canopy-active Thysanoptera in the two hedge types, although a highly significant effect of month was shown (Table 5.4).

There were small differences were seen between numbers of Psocoptera collected from Mature and New hedges and the GLM indicated no significant effect of hedge type (Table 5.4). Month on the other hand had a highly significant effect on numbers, with September apparently the most important month for both hedge types (Fig. 5.3h). The month-on-month patterns of abundance for the Psocoptera sampled at ground level and from the hedge canopies closely resembled one another (Figs. 4.2n and 5.3h).

Diptera were not caught in great number in either hedge type and appeared relatively sparse overall compared with their apparent abundance at ground level (Table 5.3; Appendix C, Table C2–C5). The GLM showed that there was no significant effect of hedge type, but there was a significant effect of month on numbers of Diptera (Table 5.4). April was the most important month for both Mature hedges and New hedges (Fig. 5.3i), with higher numbers caught in New hedges.

Nematoceran flies accounted for between 70% and over 90% of Diptera sampled from the canopy, dependent on month and hedge type (Appendix C, Tables C9 – C11), although Brachyceran flies formed a larger part of the assemblage in July. Sciarid flies were comparatively well-represented as they had been in the hedge bottoms, although Phoridae did not factor in the same way they had at ground level. Cecidomyiidae (Gall Gnats), faster-moving flies, such as Syrphidae (Hoverflies) and slower-moving Diptera, such as Tipulidae (crane fly), were rarely caught. There were some indications of 'clumping' amongst families, *e.g.* Bibionidae (notably *Bibio marci* - St Mark's Flies) were found only in New hedges in April and most Scatopsidae in one Mature hedge in September. No significant difference was found in numbers of different Dipteran groups between the two hedge age types (Mann-Whitney $U = 592.50$, $p = 0.522$).

Fewer than 90 Lepidoptera were collected in the hedge canopies (Table 5.3; Fig. 5.3j; Appendix C, Table C2) and these consisted largely of small moths, with larval forms accounting for the large part (>60%) of samples. There was a significant effect of boundary type as well as month of sampling (Table 5.4), with more Lepidoptera being collected from Mature hedge canopies than from New hedges. April was the month of greatest abundance in Mature hedges and July was the 'peak' month in New hedges.

Pulmonata were collected in low numbers (<70 in total) from the hedge tops (Table 5.3; Fig. 5.3k). April was the low point for both hedge types, and not one single specimen of Pulmonata was collected from Mature hedge canopies in April (Appendix C, Table C3). More Pulmonata were collected from New hedges than Mature hedges in every month. The

GLM showed both a significant effect of hedge type and a significant effect of month on abundance of this taxon (Table 5.4).

Dermaptera were also found in small numbers (Table 5.3) and were distributed sparsely throughout the hedge boundaries (Fig. 5.3l). Although more Dermaptera were collected from Mature hedges than from New hedges, the GLM indicated no significant effect of hedge type, but a significant effect of month was shown (Table 5.4).

Opiliones were present at very low levels, and tended to be found in marginally higher numbers in Mature hedge canopies (Fig. 5.3m; Appendix C, Tables C3 – C5). This was reflected in the GLM which showed no effect of hedge type, but a highly significant effect of month was shown (Table 5.4) with numbers being highest in September.

Abundance charts were not generated for the four 'rarest', very infrequently encountered taxa: Julida, Isopoda, Neuroptera and Polyxenida. Counts split by month are shown in Table 5.3 and further information relating to splits by hedge type and month (including ±SD and ±SE) can be found in Appendix C, Tables C3 – C5. Julida were found only in Mature hedgerows and the majority of Isopoda and Neuroptera were also found in Mature hedgerows. The two specimens of Polyxenida were found in July (Table 5.3) in a single Mature hedgerow.

5.3.3. Correlations of canopy-active invertebrate abundance with age of hedgerow in years

Spearman's rank correlations were conducted to test for the relationship between age of hedgerow in years and abundance of canopy invertebrates, both in total and by individual taxon (Appendix C, Table C12). The full set of Mature and New hedges and the smaller set of New hedges were tested separately. In view of the multiple comparisons conducted, a Benjamini and Yekultieli (aka B-Y) FDR (as described by Narum, 2006) was applied, bringing the threshold significance level down from 0.05 to 0.015. Age in years had rather weak association with canopy abundance in the majority of cases, and because of the large number of non-significant relationships, only significant results are summarised here. Data for the full range of correlations to be found in Appendix C, Tables C12 and C13.

Based on the full set of Mature and New hedgerows, age in years was significantly associated with the abundance of one taxon only in any one month: Araneae in April, with a correlation coefficient indicating a moderately negative association(Spearman's rank correlation: r_s = - 0.474, p = 0.015). The relationship between age and abundance was also negative for a number of taxa, *i.e.* Collembola, Hymenoptera, Pulmonata and

Thysanoptera, although not to a statistically significant extent overall for all months (Appendix C, Table C12).

The set of New hedgerows, for which age in years was known accurately from farm records was tested separately. Spearman's rank correlations showed a statistically significant negative relationship between age and abundance for Opiliones only for all months combined (r_s = -0.445, p = 0.003) and September (r_s = -0.703, p = 0.007).

5.3.4. Relationships between individual invertebrate taxa in the hedge top

The possibility of using the abundance of one or more 'indicator' or 'surrogate' taxa as potential substitutes for examining the abundance of the entire hedge assemblages was investigated for canopy-active invertebrates. In the same way that invertebrates at ground level were investigated for pairwise correlations between numbers of taxa (section 4.3.6), assemblages of canopy-active invertebrates were also explored for pairwise relationships. Hence, a series of Spearman's ranked correlations were conducted to test whether there were any significant relationships between numbers of individual taxa.

Taxa with very low counts were removed: ranks 14 – 17 on Table 5.3 (Isopoda, Julida, Neuroptera and Polyxenida) for all months combined were not included in the tests, and in addition in April Dermaptera, Opiliones, Psocoptera and Pulmonata were also removed from the dataset tested for correlations as none of these taxa numbered more than 6 individuals in total. An FDR (Benjamini and Yekutieli, 2001) correction was applied to the multiple correlations, giving an adjusted significance threshold of p = 0.009 for all months, July and September, and p = 0.001 for April. Correlations were initially conducted on pooled data for all months combined and for all boundaries for each individual month. Results of the top 3 correlates are shown here (Table 5.5), but fuller background data, showing values for the Spearman's rank coefficients (r_s) and significance levels for all combinations of selected taxa for all months (April, July, September) can be found in Appendix C, Tables C14–C17.

Abundance of a number of taxa from the hedge canopies was significantly correlated with that of others: three taxa each showed 9 significant pairwise correlations with other taxa, although Hymenoptera showed the strongest relationships based on coefficient values (Table 5.5), particularly with Collembola and Hemiptera. The correlations indicated a positive relationship, meaning as numbers of respective correlates increased so too did those of other taxa. There was however no relationship between any of the top 3 correlates and the abundance of either Dermaptera, Lepidoptera or Pulmonata.

Table 5.5. Correlations between abundances of canopy-active taxa for all hedgerows (Mature and New) combined (n = 83) and all months combined (April, July, September). Top 3 correlates only shown: Collembola, Hemiptera, Hymenoptera. A corrected significance level of 0.009 applies

		Top 3 correlates		
		Collembola	**Hemiptera**	**Hymenoptera**
Acari	r_s	**0.439**	**0.482**	**0.316**
	p	**<0.001**	**<0.001**	**0.004**
Araneae	r_s	**0.344**	**0.462**	**0.502**
	p	**0.001**	**<0.001**	**<0.001**
Coleoptera	r_s	**0.507**	**0.402**	**0.457**
	p	**<0.001**	**<0.001**	**<0.001**
Collembola	r_s		**0.506**	**0.629**
	p		**<0.001**	**<0.001**
Dermaptera	r_s	0.206	0.227	0.136
	p	0.061	0.039	0.221
Diptera	r_s	**0.382**	**0.354**	**0.401**
	p	**<0.001**	**0.001**	**<0.001**
Hemiptera	r_s	**0.506**		**0.660**
	p	**<0.001**		**<0.001**
Hymenoptera	r_s	**0.629**	**0.660**	
	p	**<0.001**	**<0.001**	
Lepidoptera	r_s	0.130	0.243	0.192
	p	0.242	0.027	0.083
Opiliones	r_s	**0.330**	**0.311**	**0.347**
	p	**0.002**	**0.004**	**0.001**
Psocoptera	r_s	**0.292**	**0.483**	**0.358**
	p	**0.007**	**<0.001**	**0.001**
Pulmonata	r_s	0.042	-0.004	-0.035
	p	0.709	0.970	0.753
Thysanoptera	r_s	**0.343**	**0.524**	**0.416**
	p	**0.001**	**<0.001**	**<0.001**

There was also no consistent pattern of associations between taxa month-by-month. In April there was no one taxon which was significantly correlated with more than one other taxon, and there were only 2 significant pairwise correlations (Appendix C, Table C15). Numbers of Araneae were highly significantly positively associated with numbers of Hymenoptera (r_s = 0.696, p = <0.001), and numbers of Coleoptera and Hemiptera were significantly positively correlated (r_s = 0.541, p = 0.004).

In July a greater number of significant relationships between the abundance of different taxa than in April (Appendix C, Table C16). There were several taxa whose abundance was significantly correlated with that of one or two other taxa, but two 'best' correlates were Acari and Psocoptera whose numbers were significantly correlated with

those of 3 other taxa respectively: numbers of Acari were strongly associated with those of Coleoptera (r_s = 0.612, p = <0.001) and Diptera (r_s = 0.720, p = <0.001), and with Psocoptera (r_s = 0.530, p = 0.002). Numbers of Psocoptera were significantly correlated with Acari, Araneae (r_s = 0.464, p = 0.008), and Diptera (r_s = 0.461, p = 0.009).

In September relationships differed from those seen for April and July and in fact this was the month in which there were highest number of multiple pairwise correlations.Numbers of Diptera and Hemiptera were significantly correlated with the abundance of 7 other taxa respectively in September, although these were not the same 7 taxa in each case (Appendix C, Table C17). Coleoptera and Psocoptera both showed strong positive relationships with the presence of 8 other taxa. Of the two, Psocoptera showed the stronger correlations: Araneae (r_s = 0.639, p = <0.001), Coleoptera (r_s = 0.661, p = <0.001), Collembola (r_s = 0.578, p = 0.002), Diptera (r_s = 0.727, p = <0.001), Hemiptera (r_s = 0.774, p = <0.001), Hymenoptera (r_s = 0.667, p = <0.001), Opiliones (r_s = 0.641, p = <0.001) and Thysanoptera (r_s = 0.517, p = 0.007). Lepidoptera was the only taxon whose abundance showed no correlation with that of any other taxon in any individual month.

5.3.5. Discriminating between hedge types (Mature versus New) using taxonomic abundance in the canopy

Using Sipina software (Rakotomalala, no date) Improved ChAID (Tschuprow Goodness of Split) decision tree analyses were conducted on the canopy data in order to explore the possibility of distinguishing between Mature and New hedges based simply on the abundance of a particular taxon or combination of taxa. The analysis was aimed at predicting classification into clearly discriminated hedge age groups using taxonomic abundance of canopy invertebrates. In theory, this would mean that even if we did not know whether the hedge was Mature or New, we could look at the abundances of certain taxa of the canopy and assign the hedges to one or the other grouping.

Candidate predictors of hedge age group membership were the top 10 most abundant taxa from the canopy by month (April[17], July and September) and for all months and boundaries combined (see Table 5.3). Analyses were performed on the beatings abundance data to determine whether numbers of any one taxon or combination of taxa would enable clear discrimination between the respective groups of Mature and New

[17] Only 9 taxa included in April, since 10th most abundant taxon, Dermaptera, in single figures only (Table 5.3)

hedges. ChAID splits groups entered for classification, in this case into Mature and New hedges, at points where there is the clearest separation and cases (hedges) are assigned to one or the other group depending on whether they fall above or below the number chosen as the 'splitting point'. The 'splitting point' here was a certain level of abundance depending on the taxon. The level of significance was set to 0.05 as the criterion for splitting and the default Bonferroni correction was set to Automatic.

Based on invertebrates collected in April, ChAid indicated that Acari were the only principal distinguishing taxon in terms of abundance, with a moderate goodness of split correlation coefficient of 0.444. Araneae and Hymenoptera were the second and third taxa accepted as potential candidates and entered into the model, with goodness of split correlation coefficients of 0.400 and 0.320 respectively, but did not form part of the selected decision tree as they were not as accurate in classifying cases as Acari. A classification table showed that using numbers of Acari as the basis for distinguishing between Mature and New hedges resulted in the correct assignment of all New hedges and 63% of Mature hedges to the correct age group: all 13 New hedges and 5 Mature hedges were assigned to a grouping corresponding to < 11.50 Acari, while 8 Mature hedges and no New hedges fitted the category ≥ 11.50.

In July, the ChAID decision tree identified Hemiptera as suitable for predicting membership of the two hedge types with the highest initial goodness of split correlate at 0.340 and the suggested split, New = < 13.50 and Mature = ≥ 13.50, enabled correct classification of 63% of New hedges and 93% of Mature hedges. Coleoptera were also included in the decision tree as a means of further refining the distinction between Mature and New hedges at the second level. This resulted in a rule that stated if Hemiptera ≥ 13.50 and Coleoptera ≥ 7.50 but < 41.00 then a hedge would be correctly assigned to the age group Mature in 75% of cases.

ChAID analysis on September data indicated that there were no significant distinguishing taxa which would enable assignment to respective hedge age groups. All taxa showed a very weak correlation with goodness of split coefficients ≤ 0.182.

Finally, for all months combined, analysis showed that there were no taxa whose numbers were significant predictors of membership of hedge age group. Indeed, low goodness of split coefficients indicated lack of ability to distinguish clearly between Mature and New hedges using the top 10 taxa. Acari, Araneae and Lepidoptera were the principal taxa, but were not accepted by the decision tree modelling as offering sufficient discriminatory power in assigning hedges to their groups correctly.

5.3.6. Diversity of canopy invertebrates – hedge age and taxon accretion rates

From the invertebrate count data, a number of measures of diversity were calculated to further investigate the faunal assemblages of the different hedgerow age groups and to determine whether invertebrate composition could be hedge age-dependent. Were the invertebrates of Mature hedgerows significantly different from their more recently planted counterparts at this level of assessment?

Taxon accretion/accumulation was used, not only to assess the success of sampling effort, but also to compare and contrast the 'richness' or heterogeneity of different habitats. Taxon accretion curves were generated to compare the effects of sampling effort for both hedge types for each month (Figs. 5.4). In April, Mature hedges reached their asymptote before New hedges, which themselves had not yet reached a plateau, suggesting that further sampling of New hedges would yield more taxa. A ranked ANCOVA (Quade procedure) indicated significant differences between the taxon accretion rates of Mature and New hedges for April ($F_{1,24}$ = 20.847, p <0.001). In July and September, the situation was reversed and Mature hedges showed a higher level of accretion, without levelling off. The most marked difference was evident in July: there was clear separation between Mature and New hedges and taxonomic accretion in Mature hedge canopies was above that of New hedge canopies with no overlap, suggesting that further sampling of Mature hedges would yield more taxa and thereby indicating greater taxon richness and heterogeneity amongst Mature canopies ($F_{1,29}$ = 157.387, p <0.001). In September, the accretion rate for New hedges lay well below that of Mature hedges ($F_{1,24}$ = 60.550, p <0.001).

5.3.7. Effect of time of year and boundary type on the diversity indices of canopy invertebrates

The differences in invertebrate biodiversity between hedge age types and months of sampling were further explored using standard diversity indices (as described in Chapter 3) and modelled using a GLM (Generalised Linear Model) procedure. GLM tests were used to investigate the effects of month of sampling and boundary type on 6 measures of invertebrate diversity, each emphasizing different aspects of richness, dominance and evenness. The results from the GLM provided evidence for a significant effect of month, but not of hedge type for on all diversity indices barring Heip (Table 5.6). There were differences in the level of significance: a highly significant effect was shown on Taxon Richness, whereas different levels of effect were indicated for Berger-Parker, Shannon and Simpson (Table 5.6).

Charts of diversity values for each individual index are provided to help visualize these patterns. Mature hedgerows do not appear conspicuously more diverse than New hedgerows, and do not show any less variability about median values (Fig. 5.5). Mature hedges can show larger ranges and maximum and minimum values, suggesting comparatively more heterogeneity within the group of hedgerows at times.

Taxon richness was overall higher in Mature hedges than in New hedges and peak diversity occurred in July. Taxon richness in the hedge canopies ranged from a high in July and September when a single Mature hedge yielded 14 taxa, to a low in April when only 4 taxa were collected from a single Mature hedge and a single New hedge respectively. For all months there was a greater range in values for Mature hedges than New hedges, indicating a more heterogeneous group of habitats (Fig. 5.5a). This was not the case however for all measures and Simpson diversity and evenness values tended to 'peak' in September for Mature hedges. Overall there were small differences between the hedge types, but some rather dramatic differences between months and this was reflected in the results of GLM, showing that statistically there was indeed a significant effect of month on most measures (barring Heip), but that hedgerow age group did not appear to be important (Table 5.6). Supporting data, showing the underlying summary (median, maximum, minimum, first quartile, third quartile) and on which the boxplot charts are based can be found in Appendix C, Tables C18-23.

d)

5.3.8. Correlations between canopy invertebrate diversity with age of hedgerow

The relationship between age of hedgerow and diversity value was tested further by Spearman's rank correlations (with a B-Y FDR correction of 0.018 applied) of the age in years of the hedgerows and their respective diversity scores. For Mature and New hedges combined, there was no significant association with age in years for any diversity index (Appendix C, Table C24).

Correlations were also conducted to investigate possible associations between invertebrate diversity and age of hedges for the smaller sub-set of New hedges recently-planted under AES, where age in years is known from farm records. Values for diversity/evenness indices were all negatively correlated with age, but a significant association between hedge age in years and invertebrate diversity was found only in the case of Simpson (Table 5.7).

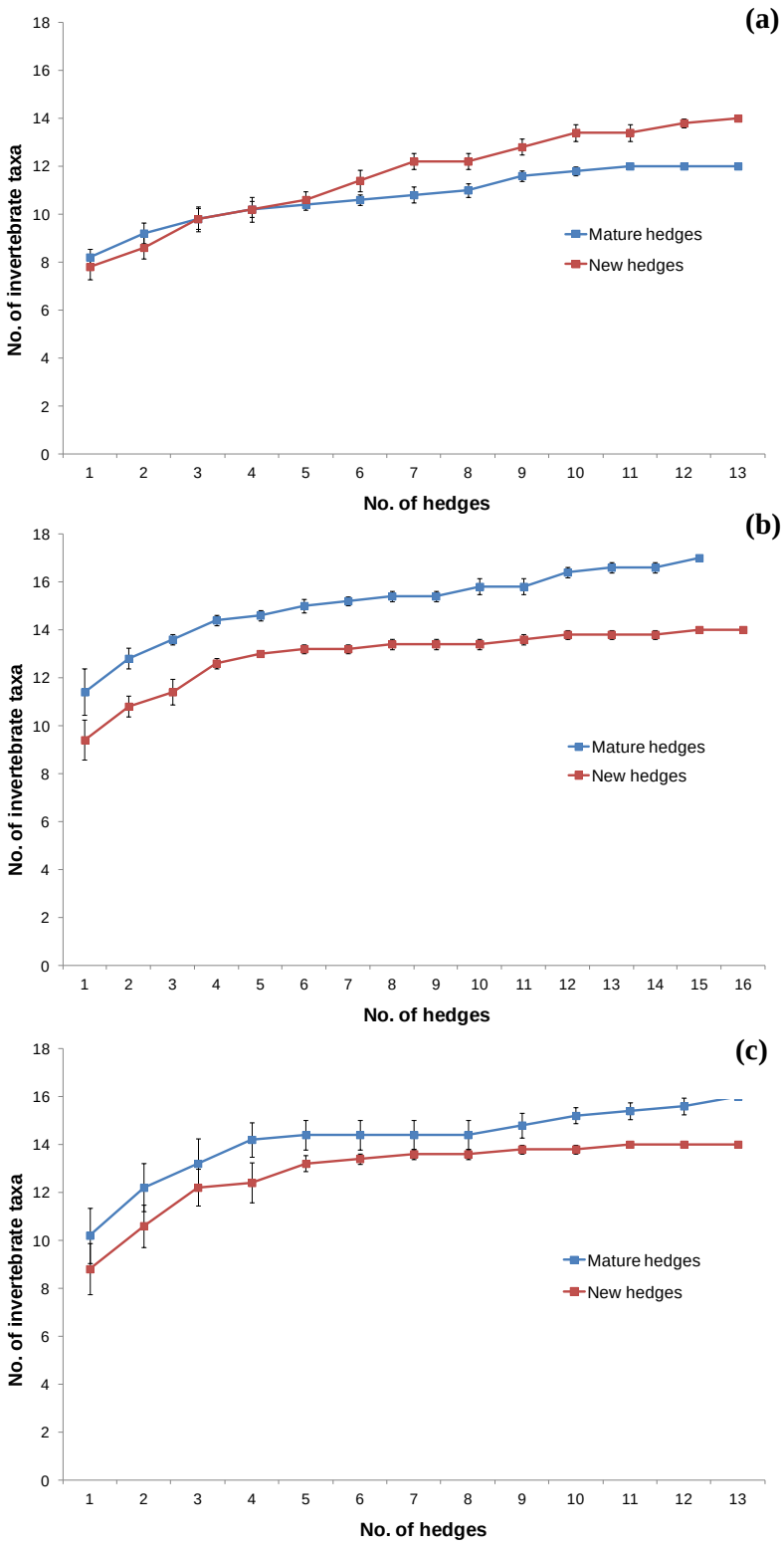


Figure 5.4a-c. Taxon accretion curves, showing the cumulative number of invertebrate taxa collected from Mature and New hedge canopies as sampling increased. Curves are shown for each month: (a) April; (b) July; (c) September. Vertical lines are ± SE

Table 5.6. Results of a Generalised Linear Model (GLM) analysis of the canopy-active invertebrate diversity of organisms collected by beating, comparing the effect of time (Month: April, July, September) and habitat (Boundary type: Mature hedges and New hedges) Values are Wald χ^2 plus significance values. Significant values at the p = 0.05 level are highlighted in bold

Diversity measure	Month		Hedge type		Interaction Month* Boundary type	
	Wald χ^2	*p*	Wald χ^2	*p*	Wald χ^2	*p*
Taxon richness	31.107	<0.001	1.200	0.273	1.462	0.481
Fig. 5.5a	**30.336**	**<0.001**	1.413	0.235	Main effects	
Berger-Parker	7.639	0.022	1.431	0.232	0.865	0.649
Fig. 5.5b	**7.636**	**0.022**	1.280	0.264	Main effects	
Shannon Diversity	10.879	0.004	1.464	0.226	1.728	0.421
Fig. 5.5c	**10.749**	**0.005**	1.252	0.263	Main effects	
Heip	2.953	0.228	0.376	0.540	3.620	0.164
Fig. 5.5d	2.755	0.252	0.217	0.641	Main effects	
Simpson Diversity	11.810	0.003	2.491	0.115	2.815	0.245
Fig. 5.5e	**11.723**	**0.003**	2.148	0.143	Main effects	
Simpson Evenness	10.854	0.004	0.928	0.335	3.636	0.162
Fig. 5.5f	**10.560**	**0.005**	0.699	0.403	Main effects	

Table 5.7. Results of Spearman's *rho* correlations between hedgerow age (years) and canopy-active invertebrate diversity for all months combined and individually (April, July and September) for New hedges only. Values are r_s plus significance values. Significant values are highlighted in bold. An FDR (Benjamini and Yekuelti) corrected significance level of 0.018 was applied

Diversity measure	All months (n = 42)		April (n = 13)		July (n = 16)		September (n = 13)	
	r_s	*p*	r_s	*p*	r_s	*p*	r_s	*p*
Taxon Richness	-0.340	0.028	-0.329	0.272	-0.163	0.547	-0.398	0.178
Berger-Parker	-0.358	0.020	-0.280	0.353	-0.364	0.165	-0.403	0.172
Shannon (diversity)	-0.327	0.035	-0.342	0.253	-0.216	0.422	-0.388	0.191
Heip	-0.097	0.542	-0.046	0.880	-0.167	0.536	0.045	0.884
Simpson (diversity)	**-0.370**	**0.016**	-0.374	0.208	-0.343	0.193	-0.415	0.158
Simpson (evenness)	-0.136	0.391	-0.057	0.853	-0.340	0.197	0.078	0.799

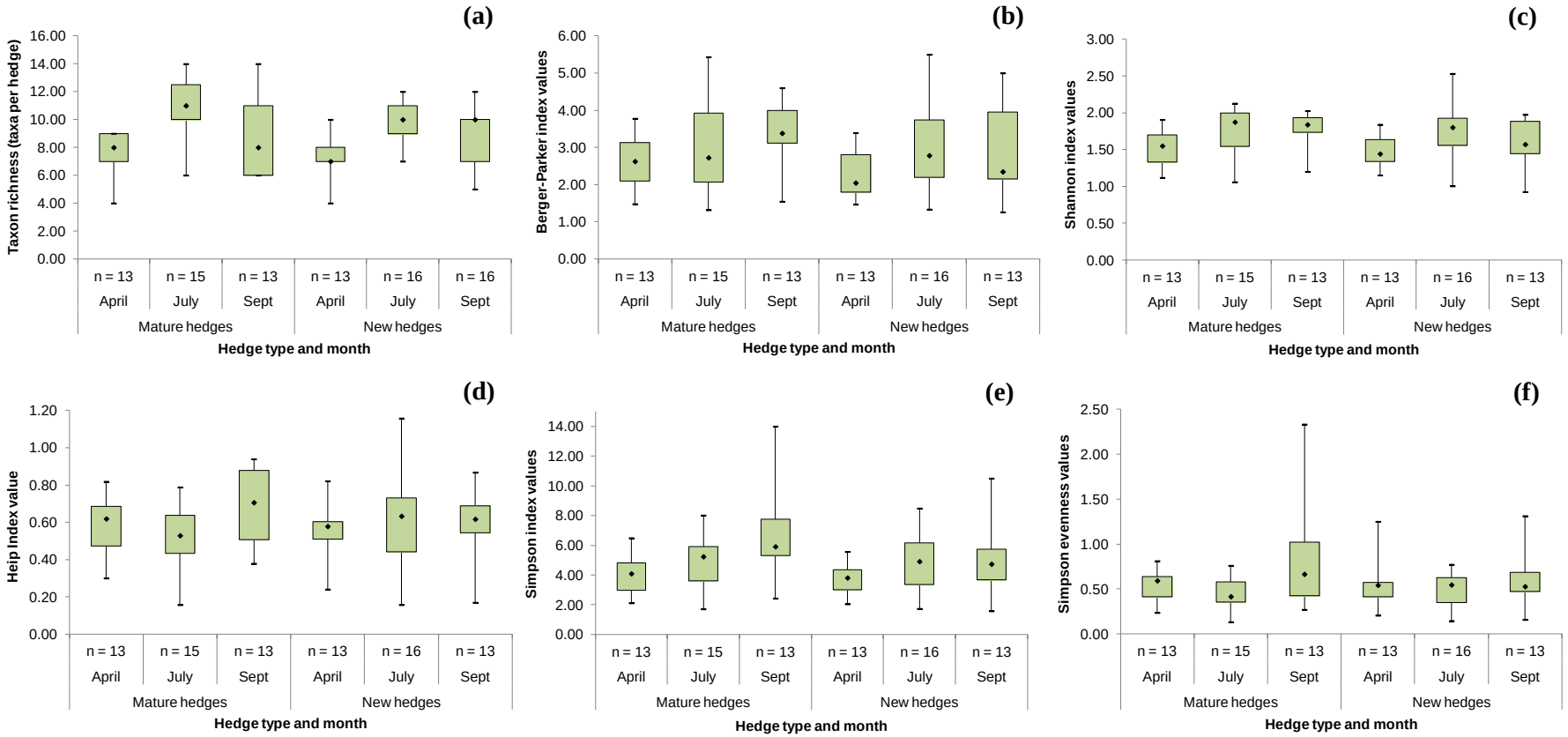


Figure 5.5 a-f. Box and whisker chart showing the median (♦), inter-quartile range (shaded box), maximum and minimum values (represented by caps on whiskers above and below box) for each month (April, July, September) and hedge type (Mature hedge, New hedge) for: (a) Taxon Richness; (b) Berger-Parker; (c) Shannon; (d) Heip; (e) Simpson (diversity); (f) Simpson (evenness)

5.3.9. Alternative indicators of invertebrate diversity in the hedge canopy

As indicated, the abundance of certain taxa has also been proposed as a means of making the process of assessing biodiversity indication more efficient, *e.g.* the finding by Anderson *et al.* (2011) that measuring the abundance of parasitic Hymenoptera has good potential as such an indicator. My own investigations had identified Hymenopterans as being a good correlate of overall taxonomic abundance both at ground level (section 4.3.6) and also at canopy level (section 5.3.6). The Hymenopteran fauna of the hedge tops largely comprised Parasitica and was not dominated by Formicidae as it had been particularly in New hedges at ground level, therefore there was no need to treat these as a separate group when conducting further investigations into their usefulness as a 'proxy' for invertebrate diversity compared with other broad taxonomic groups.

A series of correlations were performed to investigate the relationship between invertebrate abundance and diversity measures. A number of taxa showed a significant relationship with one or other of the diversity measures: 7 of the 13 taxa tested were significantly correlated with 3 measures of diversity (Appendix C, Table C25). Every invertebrate group had a significant positive relationship with Taxon Richness, but Hemiptera and Hymenoptera showed the strongest relationship in terms of the coefficient value (r_s = 0.676, $p<0.001$ and r_s = 0.643, $p<0.001$, respectively). Coleoptera was the 'best' correlate with diversity measures overall, showing significant relationships with all but Shannon (Table 5.8). The direction of the relationship was however negative, indicating a reduction in diversity as numbers of Coleoptera increased. This is likely to reflect the fact that Coleoptera, as an abundant component of the assemblage, dominated numbers and therefore exerted downward pressure on diversity scores. In all relationships, the strength of the correlation and the significance level varied to a greater or lesser degree depending on the diversity measure/taxon: Psocoptera, for instance, was the only taxon for which a positive relationship with both Shannon and Simpson diversity was shown (Table 5.8; Appendix C, Table C25).

Additionally, Coleoptera and Diptera, categorised into families/superfamilies, provided a more detailed breakdown of invertebrate diversity (Appendix C, Tables C6–C8 for Coleoptera and C9–C11 for Diptera), but numbers of taxonomic groups and diversity values thereby obtained were generally comparable with those obtained from an order-level analysis and did not show any greater discrimination between hedge types, *i.e.* Mature hedges were not shown to be superior to New hedges.

Table 5.8. Spearman's rank correlations between abundance of Coleoptera and Psocoptera and diversity (Taxon Richness, Berger-Parker, Shannon, Simpson (diversity), Heip, Simpson (evenness)) of the hedge canopy for Mature hedges and New hedges, all months combined (n = 83)

		Taxon Richness	Berger-Parker	Shannon	Simpson (Diversity)	Heip (Evenness)	Simpson (Evenness)
Coleoptera	r_s	**0.399**	**-0.283**	-0.179	**-0.393**	**-0.547**	**-0.600**
	p	**<0.001**	**0.010**	0.106	**<0.001**	**<0.001**	**<0.001**
Psocoptera	r_s	**0.613**	0.258	**0.435**	**0.284**	-0.052	-0.094
	p	**<0.001**	0.019	**<0.001**	**0.009**	0.638	0.397

Table 5.9. Total number of superfamilies/families of Coleoptera and Diptera identified from Mature hedge canopies, New hedge canopies for April (n = 13 per hedge type), July (n = 16), September (n = 13). Abbreviations: M = Mature hedge, N = New hedge, H = Hedgeless

	April		July		September	
Taxon	**M**	**N**	**M**	**N**	**M**	**N**
Coleoptera	12	13	10	13	7	6
Diptera	5	11	12	8	7	7

A total of 17 Coleoptera (super-)families were collected from the hedge tops by beating and 20 (super-)families of Diptera were found, but were not all present in every month in both hedge types. There were fewer groups of beetles and flies represented in the samples from the hedge tops than hedge bottoms: on average (across months and hedge types) 6 fewer beetle (super-)families and 13 fewer fly taxa were found in the hedge canopies than at ground level.

There were not consistently more family groups (Taxon Richness) in Mature hedges for Coleoptera and Diptera for all months (Table 5.9; Appendix C, Table C26 a-c). In every month there were Coleopteran and Dipteran families which were found in both hedge types, generally the majority, but there were also a number of taxa which were sampled only in either one or other hedge type.

Diversity measures were not consistent in the way they 'ranked' the hedges depending on month and taxon and in July, although sheer number of taxa was lower in Mature hedges, because of the more even distribution of organisms amongst the categories, indices valued Mature hedges higher. Whether one or the other hedge age type might be considered more diverse depended upon the measure. Mann Whitney *U* results indicated a clear difference between Mature and New hedges for the Berger-Parker and Simpson values for Dipteran fauna (both n = 3, Mann-Whitney $U = 0.00$, $p = 0.05$), with New hedges showing consistently higher values for all months (Appendix C, Table C26a–c).

There were however no other significant differences between either beetle- or fly family diversity of the respective hedge age groups by other measures.

The values achieved by using families of Coleoptera or Diptera were not greatly different from values achieved by using order, but involved a considerable increase in identification and classification effort over order. There was some increase in discriminatory power, indicating that Dipteran family diversity in particular could be quite different between hedge age types.

5.4. Discussion

Results from the sampling of the hedge canopies by beating indicated that there was no statistically significant difference overall between the invertebrate abundance found on Mature and New hedges, although month of sampling was significant. This mirrors the finding for invertebrate abundance in the hedge bottoms. In contrast to the invertebrates sampled in the hedge bottoms, overall diversity values of canopy invertebrates appeared not to be affected by hedge age, but were significantly affected by month for all diversity measures, excepting Heip. Further analysis of certain groups below order level showed differences in diversity between the different hedge ages, but the level of difference shown was dependent on the diversity measure chosen.

5.4.1. Mixed responses to hedge age by canopy invertebrates

The relationship between age and abundance was weaker than had been the case for invertebrates captured at ground level on sticky traps. Although a significant effect of hedgerow maturity could not be demonstrated on either the abundance or diversity of canopy invertebrates generally, a significant effect of hedge age on the abundance of a few individual taxa was shown, namely Acari, Hemiptera, Lepidoptera and Pulmonata. In addition, although 'seasonal' differences were widespread, effect of month on abundance was not universal for all individual taxa, *e.g.* Araneae appeared indifferent to time of sampling at canopy level, by contrast to Araneae at ground level. The taxa affected and the nature of the effect differed from those seen in taxa of the hedge bottom, adding to the mixed picture of benefits to invertebrates.

Analysis of Coleopteran and Dipteran families suggested a 'complementary' relationship between New hedges and Mature hedges, best illustrated by looking at examples from the beatings data. In July, for instance, 13 Coleopteran families were identified, of which 10 were common to both hedge age types, 3 were found in very low numbers only in New hedges and none were 'unique' to Mature hedges. Also in July, 12

Dipteran families were identified, of which 4 were shared, 6 were found only in Mature hedges and 2 in New hedges only. There were distinct differences in the taxa, which appeared also to be seasonal. This suggests that younger hedge habitats might offer good living conditions for certain organisms, at certain times of the year, while more mature hedgerow habitats offer other qualities to different fauna, just as young stages of growth in coppiced woodland offer sometimes preferential habitat for different invertebrates compared with older growth (Fuller & Warren, 1993). In order to account for such differences in the hedge canopy however comment is made on the possible importance of various factors besides habitat 'maturity' *per se*. Explanatory variables are not reported here, but are examined in further detail in Chapter 6.

5.4.2. Invertebrates of hedgerow canopies – a neglected theme?

Whereas the invertebrate fauna of the farmland hedge bottom have been studied extensively, Pollard & Holland (2006) noted that studies which have attempted to describe the diversity of invertebrates in the hedge itself (the woody element) were comparatively few (citing Lewis, 1969; Pollard, 1974; Hradetsky & Kromp, 1997, Maudsley, 1997 & 2002). Even Pollard & Holland's (2006) work was based on data collected nearly a decade earlier. This apparent deficit is perhaps surprising given the extent of hedgerows as a semi-natural habitat and their supposed importance in preserving farmland biodiversity. Also, considering the popularity of hedgerow options amongst UK farmers under agri-environmental schemes (Boatman *et al*., 2008; Ledder, no date), exploration and understanding of how invertebrate populations respond to the creation and management of new hedgerow habitat seems strangely lacking. Contributions to our current understanding of the invertebrate fauna of the woody element of farmland hedgerows still appear scarce, although the influence of management techniques on invertebrate communities of hedge canopies have recently been explored at the NERC Centre for Ecology and Hydrology (Amy *et al*., 2015). There is therefore relatively little comparable literature on which to draw to help explain patterns seen in this study.

In the absence of much research relating to the woody part of the hedgerow, forest canopy studies have been used as a supplementary source of information for invertebrate distributions (*e.g.* Floren & Schmidl, 2008). The dearth of published woodland canopy studies describing UK conditions, however, also means looking further afield, and while acknowledging the difficulty of making direct comparisons, this can have value in contextualising 'woody' ecology. Another caveat is undoubtedly the extent to which the woody element of a hedgerow could be regarded as resembling actual woodland, and may

be dependent on connectivity with a 'source' woodland (Dennis, 1997). Hedgelink (no date a) defines hedgerows broadly as "linear woodland edges", capable of harbouring at least some woodland invertebrate species in otherwise intensively cultivated farmland (*e.g.* Gruttke & Kornacker, 1995; Fischer *et al.*, 2013). For certain taxa, including species of parasitoid wasp (which accounted for the majority of Hymenopterans collected by beating in this study), moth and gall-forming midge, they may even provide similarly favourable (or tolerable) conditions to woodland proper (Dennis, 1997). If hedgerows are indeed woodland edges, then populations might be subject to 'edge effects', resulting in a rather 'dynamic' environment with consequences for assemblage composition and abundance (Dennis, 1997). Such dynamism, presumably even more pronounced in the canopy of the hedgerow than in the relatively sheltered hedge bottom, makes gaining a 'representative' view of the fauna of hedgerow canopies difficult. This helps explain why studies of the hedge canopy are relatively uncommon compared with the ground level.

Edge effects are recognized as playing an influential part in determining numbers and types of canopy invertebrates. Invertebrates in woodland edges are exposed to much higher levels of disturbance by environmental influences (notably temperature, moisture and light) than woodland interiors, which have a potentially deleterious effect on abundance and diversity (Dennis, 1997; Didham, 1997; Ozanne *et al.*, 1997). In addition to disturbance by environmental influence, an arable farmland hedgerow also has to contend with regular disruption as a result of agricultural activities in adjacent crops, thus contributing even further to the 'dynamics' (maybe instability) of the invertebrate assemblages. An exposed canopy will presumably be even more 'dynamic' than the more sheltered hedge bottom, with many more flying visitors or transient species. Disturbed conditions would also tend to favour adaptive generalists on the whole (Didham, 1997). This could account at least in part for the generally lower abundance and smaller number of taxa and lower diversity of invertebrates in the woody part of the hedge as opposed to the hedge bottom in this study, differences in sampling method notwithstanding.

Research in forest entomology using consistent sampling techniques suggests that broad insect assemblages (order level) are indeed considerably more abundant at ground level (Preisser *et al.*, 1998). Studies on the invertebrate fauna of deciduous forests in Canada, found that insects and spiders were overall more abundant in the understory compared with the canopy (Larrivee & Buddle, 2009; Buddle, 2013). It is perhaps logical that more insects and spiders are found closer to the ground, given that tree canopies "are relatively harsh environments" and can be "windy, hot and often dry" compared with the

forest floor (Buddle, 2013). In the same way, hedgerow canopies will presumably tend to be more exposed to harsher climatic conditions than the hedge bottom and this will affect the presence or apparency of invertebrates in the woody element of the hedgerow. Chapter 6 examines the effects of climatic conditions on invertebrate assemblages of both hedge bottom and hedge canopy.

5.4.3. Taxa exhibiting greater abundance in Mature hedge canopies

Acari were found in greater numbers in Mature hedges than in New hedges, but were not as dominant in the canopy as they had been at ground level. Joyce *et al.* (1997) indicated that their abundance in the hedgerow canopy was conspicuously lower than for other major groups accounting for around 3% of invertebrates, compared with 8% overall in my study. Pollard & Holland (2006) excluded Acari (and also Collembola and Thysanoptera) from their study of hedgerow arthropods, which may be for the same reason Floren (2008) cites, *i.e.* that small arthropods can vary greatly in numbers between samples as a result of more or less effective sampling and these large variations in densities may create difficulties in data analysis and interpretation.

Oribatid mites, which were (by observation) well-represented amongst the Acari, are known to be one of the most abundant groups in temperate forest canopy habitats, if not the most abundant group (Sobek *et al.*, 2008). Compared with woodland, hedgerows may simply not be particularly good habitats for arboreal Acari in general. Differences in sampling technique might explain why Acari appeared so much less dominant in assemblages of hedgerow canopies than in assemblages of forest canopies. Sobek *et al.* (2008) used a 'non-invasive' branch-rinsing technique which might have been more effective at dislodging organisms than the beating technique I used, and might be appropriate in a targeted follow-up study.

Investigating the canopy fauna of Central European mixed forest, Sobek *et al.* (2008) found that oribatid mites were more abundant and diverse in trees with more complex bark structure and thicker branches, such as larch and spruce. Hedgerow shrub species may not behave in the same way as these tree species, but have woody structures that are likely to offer at least some suitable habitat for Acari. Bark structure is known to have a strong effect on arboreal micro-arthropod assemblages in particular (Nicolai, 1986). If, as Sobek *et al.* (2008) showed, the highest numbers of individuals are to be found on thick branches, then a likely explanation for the apparent preference of Acari for Mature hedge canopies is that these habitats offer better-developed woody structures than New

hedges, and therefore more favourable 'architecture' with thicker branches, larger surface area and more complex bark structure.

Significantly more **Hemiptera** were also found in Mature hedges than in New hedges, presumably because of the larger woodier canopies associated with mature hedges, providing a greater quantity and more varied living space. Floren (2008) recorded a greater abundance of Hemiptera in older tree canopies than newer tree canopies (80- versus 8-year-old spruces). Although not reported directly, there appeared to be a bias in catches towards aphids, psyllids and leafhoppers/froghoppers, as there had been at ground level, but the relative proportion of Heteropteran taxa (including predatory groups) was higher than in the hedge bottom. Foliage biomass may have been an important factor also in this, although a measure of density was taken, rather than direct calculation of foliage biomass (Chapter 6). Amy *et al*. (2015) found that structural factors were more important to herbivore abundance than nutritional quality of foliage.

Significantly more **Lepidoptera** were found in Mature hedgerows than in New hedgerows, but overall their abundance, or incidence, was relatively low by comparison with other taxa in the assemblage (1% of total), comprising largely larval forms (60% in total) and small moths. Similarly, Pollard & Holland (2006) collected comparatively few Lepidoptera from the 13 hedges they sampled, accounting for around 1% of the total assemblage. Joyce *et al.* (1997) also found that Lepidoptera were scarce in the hedgerows they fogged, forming <1% of total, corroborating a view of sparsity of Lepidoptera in farmland hedgerows. A study using a light box (for moths) and observational techniques (for butterflies/day-flying moths) might have yielded more organisms, although data collected via visual transects conducted along some of the same farmland hedgerows (R. Farrow, unpublished), also indicated a very low abundance of Lepidoptera. Lepidoptera were more abundant in Mature hedgerows, but low numbers seen here (<100 in total for all 3 months) might reflect populations struggling to find suitable habitat in the farmed environment. Barr *et al*. (2005) note that many Lepidoptera have hawthorn as a food plant and therefore hedgerows should be an important habitat, but some research suggests other measures besides AES hedgerow options would better support Lepidopteran abundance and diversity, such as species-rich grasslands and increased emphasis on woodland creation (Fuentes-Montemayor, 2011 a & b).

Why Mature hedgerow canopies should offer superior conditions for Lepidoptera is unclear, although a better developed growth form, offering greater shelter might help explain the difference (Dover *et al*., 1997). Dover (1996) found that butterflies were more

common at intersections of hedges and woodland where the microclimate was more stable in terms of temperature and humidity. Finding stability and shelter from disturbance through fertilizers, pesticides and wind is presumably important for these organisms, as Barr *et al.* (2005) indicate. Many moth species (as well as butterfly species) are known to have a preference for woodland (Chinery, 2007), so would presumably prefer the woodier habitat offered by a mature hedgerow. Floren (2008) collected a greater abundance of Lepidoptera from older tree canopies than new spruce tree canopies (80- versus 8-year-old).

5.4.4. Taxa exhibiting greater abundance in New hedges

Reasons for the significantly higher numbers of **Pulmonata** (pulmonate snails) in New hedges than Mature hedges are unclear, but suggest that New hedges are capable of providing suitable living conditions and sufficient shelter and shade, despite their generally smaller canopies and smaller stature than Mature hedges. Opportunities to shelter and avoid direct sunlight are important determinants of snail distribution (Jones & Jones, 1984). Another important determinant of numbers is availability of food and perhaps the results in this study suggest that more favourable feeding conditions are likely to occur in New habitats. Mature hedges were sometimes associated with less compact canopies and sparser foliage due to woodier outward growth and so sheer 'apparency' of snails may also have been lower.

Month of sampling had a highly significant effect on snail abundance, with numbers reaching their highest in July. Episodes of wet, warm weather in July and attendant increases in humidity within the hedgerows may have encouraged an increase in their abundance in the hedge canopies, as activity is known to be positively correlated with moisture levels (Cameron, 1970, 2003). Rain can thus be an influential factor in determining snail activity levels (Jaremovic & Rollo, 1979; Mensink & Henry, 2011). Also, snails consume fresh material to compensate for water losses (Mensink & Henry, 2011), and so greater activity (abundance) in high summer should not be regarded as unusual.

5.4.5. Taxa exhibiting effect of month but no effect of hedge type on abundance

The majority of invertebrate taxa showed no significant preference for either Mature or New hedges. There may be a number of explanations for this connected with the differing ecologies of the groups involved. For some taxa it seemed surprising that no significant association with hedge maturity could be found (*e.g.* Psocoptera), for others, particularly more vagile flying taxa able to evade capture and move with ease amongst

habitat resources, maybe less so. There is a sense that the large speciose groups, such as Coleoptera, Diptera, and Hymenoptera, are so adaptable in general to differing and unstable farmland environments that they just as easily cope with a range of habitat conditions, meaning there will be no obvious difference between distributions in hedge types. A point to bear in mind regarding apparent lack of differences in abundance distributions between the hedge age groups, is the fact that a similar volume of hedge was sampled in both types of hedge, not the canopy as a whole. Mature hedges tend to be greater in size and so invertebrate numbers in the canopy are likely to be greater overall than in newer hedges that lack bulkier crowns. Scaling to account for superior hedge height was not undertaken as Amy *et al*. (2015) have done, since it was felt that this would make too many assumptions about the uniformity of living conditions in different parts of the hedgerow.

Collembola (springtails) were the most abundant taxon in both the hedge bottom and hedge canopy. More were collected from New hedges than Mature hedges in total, but there was no statistical difference in numbers. Just as Collembola at ground level were not significantly associated with either hedge age group, so springtails collected from the canopy seemed indifferent to hedge age. This may be a reflection of their ubiquity and super-abundance in terrestrial environments (Hopkin, 2007). Collembola can be abundant in arboreal environments, particularly in broad-leaf canopies (Hopkin, 2002 & 2007; Tovar-Sanchez, 2009). They can also vary greatly in number between trees in both tropical canopies and also in temperate forests (Linsenmaier *et al*., 2001; Floren & Schmidl, 2008). In terms of feeding opportunities, young hedges may be just as likely to offer suitable fodder (algae, fungal spores, decaying vegetation) as mature hedges and also be capable of offering essential levels of humidity at canopy level.

Coleoptera were more abundant in New hedges than in Mature hedges overall, but not enough to show a significant effect of age on abundance. Month on the other hand was important for Coleoptera, with highest abundances achieved in April in Mature hedges and in July in New hedges. The lack of significant effect of hedgerow age corresponds with findings by Pywell *et al.,* (2005), albeit at ground level: although they found hedgerow Coleoptera responded differently to hedgerow age, with certain species preferring young hedges and others mature hedges, there was no significant preference overall for habitat of a particular age. Borrowing from forest ecology once again, Floren (2008) found mixed evidence for the effect of age on the abundance of Coleoptera in forest canopies. He found

that Coleoptera were generally more abundant on younger oak, with numbers declining with age, but by contrast more abundant in older spruce.

Regarding the effect of month, Mature hedges may be preferred for overwintering by certain abundant taxa and may be capable of sheltering greater numbers of invertebrates earlier in the year. Because of their stage of development, they presumably offer preferential conditions to younger less developed habitats at a time of year when weather is arguably less stable than summer. Conversely, younger hedge habitat might be preferred by certain species for different qualities and reach peak activity-density during the summer, perhaps due to increased visitors. Different families/species thrive under different conditions, determining their preference for mature or younger habitat types, but due to the broad taxonomic approach in my study this is 'masked'. Further investigation of Coleoptera at family level suggested that different groups may have a preference for different types of hedge, whereby newly-planted hedges form a 'complementary' habitat to established Mature hedges.

Latridiidae (the family of 'mould' beetles) and Curculionidoidea (the superfamily of weevils) dominated the Coleopteran fauna in this study. Latridiidae were well-represented, as they had been at ground level, and were in fact the most abundant family overall in the canopies. Curculionoidea, the weevil superfamily, were also well-represented and were the most abundant group in the summer. There was little to choose between numbers of Latridiidae collected from Mature hedges and numbers collected from New hedges. Curculionoidea were more abundant in New hedges and Chrysomelidae (leaf beetles) in Mature hedges. A possible explanation for the presence of more Chrysomelidae in Mature hedges may be the generally larger canopies with more abundant foliage. It is unclear why weevils, many of which also feed and oviposit on and in living plant tissue, and include some pollen-eaters and fungivores (Barnard, 2011), might prefer New hedges. At least part of the apparent preference of Curculionoidea (in particular pea/bean weevils) might be accounted for by the proximity of bean crops to several of the New hedges and in addition an abundance of Trifolium, such as Clover, Vicia (Vetches) and other members of the Fabaceae (Legumes) in the margins. Sampling in July, Pollard & Holland (2006) found that Curculionidoidea were the largest group of beetles in the hedge canopy, as did my study. Latridiidae did not however figure as prominently amongst Pollard & Holland's hedgerow arthropods and were lower in abundance than most other Coleopteran families. Pollard & Holland (2006) sampled only in July, but had they sampled in spring, they might have discovered an abundance of Latridiidae. Although Latridiidae are generally called

'mould beetles', Barnard (2011) indicates that they can be found on flowers and indeed they were very much in evidence on hawthorn blossom during the spring sampling in this study. Other Coleopteran taxa were not collected in such high numbers as Pollard & Holland (2006) achieved with fogging on fewer hedgerows.

Joyce *et al.* (1997) found that hedgerow Coleoptera quickly returned to pre-spray levels only 30 days after chemical knockdown. This helps demonstrate the excellent dispersal and colonisation ability of beetles in general and their ability as a group, with many different life histories and feeding habits, to adapt to a wide range of habitats (Barnard, 2011). Pawson *et al.* (2011), in another illustration of the adaptability and dispersal ability of beetles as a group, found that populations subjected to clear-felling returned to pre-disturbance levels after only 8 years. Their huge variety may help explain why in this study they show no preference for hedge age type.

Dermaptera were marginally more abundant in Mature hedges than in New hedges in this study, but no statistically significant difference was shown between the two age groups. Numbers of Dermaptera were low overall, which is perhaps unsurprising, given that they are essentially ground-living and seemingly reluctant to fly (Chinery, 2007). They are however apparently capable climbers and can scale vegetation to feed on, for example, plant leaves and flower buds (Jones & Jones, 1984; Barnard, 2011), and in autumn could have to do with mate-seeking (Capinera, 2010). Joyce *et al.* (1997) and Pollard & Holland (2006) also found low numbers in hedgerows. This also reflects the fact that, although Dermaptera are evidently capable of venturing opportunistically above ground into the canopy of hedgerows, it is unlikely to be their preferred habitat. Dermaptera are another example of a taxon more likely to be nocturnally active and so under-sampling due to time of day is possibly a contributory factor in low numbers.

Diptera were almost equally abundant in New and Mature hedges, with just a handful more being found in Mature hedges. By contrast, Floren (2008) found that Diptera were most abundant in the canopies of the oldest tree stands. My study found Diptera to be rather less important in terms of the proportion of total invertebrates in hedgerows than shown by Pollard & Holland (2006), accounting for only 4% versus 9% of the assemblage. Joyce *et al.* (1997) also reported a higher proportion of Diptera, finding that they accounted for 15% of the total assemblage. The difference between my study and published data might be ascribed to an extent to a combination of sampling method and dispersal capability of members of this group: escapees from the beating funnel were observed. Faster-flying Diptera such as members of the sub-order Brachycera (which include

hoverflies, houseflies, blowflies *etc*) were not collected in any great number. Likewise, relatively few hoverflies or houseflies were collected by Pollard & Holland (2006), despite using a chemical knockdown technique. The implication is that these taxa were capable of evading capture and/or were not generally abundant in hedgerows themselves. Peng *et al.* (1992) found flying insects were distributed at different vertical levels of hedgerow trees, with fungivores such as Mycetophilidae lower down than other Dipteran families. This differential distribution will also influence catches.

Dipteran fauna in my study were dominated by Nematocera (midges, gnats, mosquitoes), many of whom are acknowledged to be delicate, weak flyers (Oosterbroek, 2006; Barnard, 2011). Sciaroidea (superfamily of fungus gnats), which are rather sedentary, not moving far from their breeding sites (FCMCD, 2006), were particularly well-observed, just as they had been in samples from the hedge bottom. Sciaridae were the largest sub-group overall. Sciarid flies were also the most abundant group of Diptera recorded by Pollard & Holland (2006).

Month of sampling has a significant effect on numbers of Diptera. In both hedge types abundance was highest in April, and not July. This might be counter to expectations of peak activity in summer and is likely to have been caused by the dominance of Sciarid flies. Mohrig & Blasco-Zumeta (1995) found that spring was the best season for collecting Sciaridae from forest vegetation.

Hymenoptera were more abundant in Mature hedges than New hedges, although not to a significant degree. Month was important, with July being especially important for Mature hedges and to a lesser extent New hedges. This tallies with a presumed period of optimum activity relating to potential hosts/prey.

Hymenoptera were not such an important component of the assemblages of hedgerow canopy invertebrates as they had been of hedge bottom assemblages in this study. There were no accumulations of Formicidae, as there had been at ground level. In the canopy, Hymenoptera appeared to be largely composed of parasitic groups (Parasitica made up more than 80% of the total number of Hymenoptera) and this may help account for the relative indifference of Hymenoptera to hedge maturity. Their immense speciosity (Barnard, 2011) means that collectively they might just as easily find favourable, or at least tolerable, conditions – *e.g.* suitable types and numbers of hosts - in a New hedgerow as a Mature hedgerow. Also, location of hosts such as insect eggs, caterpillars, aphids and immature stages of flies may involve ambulatory searching or even waiting (Vinson, 1998). Parasitoid hymenoptera are known to adopt a reduced walking speed when

searching for suitable hosts in complex environments (Rehman, 2010) and this doubtless affects their apparency and abundance in hedge canopies, making them perhaps quite vulnerable to collection by beating compared with other faster flying Hymenopterans and other winged taxa.

The seeming absence of bees, wasps (and other pollinators) at canopy level could also reflect the fact that conditions for foraging on the hedgerow itself may not be suitable. This makes sense since hawthorn-dominated hedges blossom in May and offer no other floral resources themselves throughout the season for nectar and pollen feeders, unless they have been planted with other flowering species, such as Guelder Rose (*Viburnum opulus*), or have been 'colonised' by Blackberry (*Rubus fructicosus*), Dog Rose (*Rosa canina*) or climbers such as White Bryony (*Bryonia alba*).

Like Hymenoptera, marginally higher numbers of **Opiliones** were found in Mature hedges than in New hedges, but there was no significant difference between the two hedge age groups. Abundance of Opiliones was significantly negatively correlated with age in years: reasons for this are uncertain, but the effects of growth stage on complexity are discussed with regard to Araneae (also negatively correlated with age) below which might also have a bearing on Opiliones as arachnids. Month of sampling was significant in determining numbers of Opiliones and September was the most important month irrespective of hedge age type. This fits the harvestman lifecycle, whereby peak activity/density is reached in late summer/autumn (Richards, 2010).

At ground level also this study found no effect of hedgerow maturity on the presence of harvestmen in general. Their apparent indifference to type of hedge might be attributed at least in part to their catholic eating habits. They consume a wide variety of items, including many invertebrates and also plant materials (Bristowe, 1949; Richards, 2010) which might be found in a range of habitats.

Opiliones were found in much lower numbers in the hedgerow canopies than at ground level. Like Neuroptera, Opiliones tend to be nocturnal, hiding in moist places during the day (Richards, 2010), and so daylight sampling may lead to their under-representation in catches. Richards (2010) indicates that there are climbing species, and Proud *et al.* (2012) highlight the fact that ground-dwelling species may undertake vertical migration during the day, descending into leaf litter at dusk to forage. Joyce *et al.* (1997) and Pollard & Holland (2006) also found that Opiliones were relatively uncommon in the woody part of the hedge.

Of the work on forest canopy entomology, Floren (2008) does not report explicitly on Opiliones in his study of differently aged woodland. None of the other studies in Floren & Schmidl's (2008) volume of canopy research includes Opiliones, suggesting that the group is not an important component of the invertebrate fauna of temperate forest canopies. Proud *et al.* (2012) conducted a study of Opiliones in tropical forest, sampling by hand during the daytime and at night. For diurnal samples, Proud *et al.* (2012) did not detect any differences in relative abundance, species composition, or species richness between three different forest ages. In contrast, from nocturnal samples, they observed minor differences in relative abundance (and species composition) among the three successional forests. Primary forest and young secondary forest showed the greatest differences in species composition, while mature secondary forest was relatively similar to both. Some ground-dwelling species showed a preference for young forest and some mature forest (Proud *et al*, 2012).

Indications from sticky trapping were that numbers of **Psocoptera** collected at ground level were significantly associated with Mature hedges, but this was not the case for the canopy environment. This seemed rather counterintuitive for barkflies: we might assume that mature hedgerow habitats generally capable of offering larger areas of bark and canopy foliage would be favoured over newer hedges, but Psocoptera were only marginally more abundant in Mature hedges at canopy level. Beating is the conventional way of sampling Psocoptera in the canopies of trees and bushes, but it is effective only for branches and not trunks. Sampling of the trunk/stem was not included. In fact, bark brushing is also recommended to ensure the bark on the trunk is adequately sampled (BRC, no date). There are obvious issues with a 'bark brushing' method in thorny hedgerows, and even a modified 'washing' technique may not be practical, but could be considered for a study targeting Psocoptera.

Although sampling effect is likely to have had a considerable influence, a contributory factor in the abundance of Psocoptera may have been availability of food or of sites for oviposition. For example, perhaps suitable 'adventitious matter' for Psocoptera to feed on, *e.g.* fungal spores and hyphae, algae, pollen and animal remains (New, 1970), is just as likely to be accessible on leaves from new hedges as mature hedges. More recently, Saville (2010) found that crustose and foliose lichens can be important to Psocoptera for grazing and egg-laying. In particular, certain Psocoptera feed preferentially on the foliose lichen, *Xanthoria parietina*. *Xanthoria parietina* is tolerant of high levels of nitrogen in the environment and considered an indicator of agricultural pollution. The species could

arise in any hedgerow exposed to high nitrate inputs and was often seen on hedges of both age types during hedgerow survey work conducted for this study. New (2005b) downplays the significance of lichens in the diet of Psocoptera and implies that fungi may have a greater role and this might help explain the increase in abundance of these organisms as the seasons progress.

Month of sampling had a significant effect on the abundance of Psocoptera in this study. The seasonal pattern of abundance for Psocoptera was very similar for both hedge types, showing very low abundance in April, higher abundance in July and highest abundance in September. This seasonal pattern links with New's (2005b) observations regarding the seasonality of food availability for arboreal psocids. Although food supply on the bark is often abundant, with some seasonality, food supply in the foliage of tree (and by extension hedge) canopies shows a strong seasonal development. Food supply on the surfaces of deciduous tree leaves is lacking early in the season, but then increases over the life of the leaf. For Oaks (*Quercus* spp.), New (2005b) found an increase in food over the summer months into autumn, correlated with an increase in foliage-frequenting Psocids in late summer. The Biological Records Centre (BRC, no date) indicates that in general Psocoptera appear in late summer and autumn and August and September are the best months for recording Barkflies. The increase in food can partly be explained by the honeydew moulds that arise as a result of the excretions of herbivorous Hemiptera (New, 2005b).

Despite the reported attractiveness of hawthorn and other hedgerow species to Psocoptera (New, 1970), compared with woodland canopy studies (Floren, 2008), numbers of Psocoptera collected in this study were moderate. Pollard & Holland (2006) also found Psocoptera to be markedly lower in abundance than the 'big five' most abundant groups Araneae, Coleoptera, Diptera, Hemiptera and Hymenoptera in hawthorn-dominated hedgerows. Hedgerows might ultimately be a suboptimal habitat for Psocoptera on the whole, but it is difficult to know how one could enhance conditions. It seems that the best option for conserving this group is not hedgerow planting, but perhaps tree planting and retention and expansion of woodland proper.

Thysanoptera were marginally more abundant in Mature hedges but there was no significant difference between hedges of either age, patterns of abundance through the months being virtually identical. Szeflinska (2004) compared the Thysanopteran fauna of shelterbelts (tree lines) of different ages in arable farmland. She found that 7/8 year-old shelterbelts already showed assemblages of Thysanoptera comparable with 100-year-old

shelterbelts, suggesting quite rapid achievement of a 'climax' population of Thysanoptera. Very young shelterbelts (2 years old) were different from the more mature shelterbelts and were characterised as 'dynamic' rather than stable.

Month was of great significance to Thysanopteran numbers and July was the month of highest abundance in this study. Since Thysanoptera feed on a variety of living plant matter, including flowers and leaves, and some are also predatory on small insects and mites (Barnard, 2011), it follows that they will experience a population surge in times of high food availability. Fungi/fungal spores also form part of their diet. Fungi can occur wherever humidity and temperature is favourable and can seem to arise out of nowhere and they are therefore just as capable of occurring on young as mature foliage and at different times of the year. The ubiquity of suitable food stuffs and their wide dispersal ability may account for the lack of conspicuous difference between numbers of Thysanoptera in Mature hedges and New hedges. Thysanoptera can disperse readily throughout the environment in great numbers, not only because they are winged organisms, but because their small size means they are easily wind borne.

5.4.6. Taxa exhibiting no effect of hedge type or month

Although catches of **Araneae** were greater in New hedges, this was not to any significant extent and overall they were seemingly indifferent to hedge age or month of sampling. This may reflect their wide abundance and dispersal capability (Jones-Walters, 1989; Roberts, 1996). Joyce *et al*. (1997) stated that they are "often the most abundant invertebrate in the hedgerow", with small species being able to disperse well (through ballooning), although neither their study nor Pollard & Holland (2006) showed that they were the most abundant taxon in the hedgerow canopy. In fact, Araneae, despite being collected in relatively large numbers in both studies, and accounting for a high proportion of the assemblage, were far outweighed by the most abundant taxon, Hemiptera. In this study, Araneae were also considerably lower in number than Hemiptera, Coleoptera or Collembola, the three most abundant taxa in the hedge canopies.

The seeming indifference of Araneae to the type of hedgerow is in keeping with findings from sticky traps, which showed that Araneae seemed to prefer grassy, hedgeless boundaries. Ysnel & Canard (2000) found that the species richness and species composition of dominant spiders was the same for hedges of different quality and their findings also suggest that Araneae are not 'particular' about type of hedgerow. Interestingly, Floren's (2008) findings from forest canopy research also seem to corroborate a view of Araneae as essentially 'unfussy' regarding the nature of woody

habitat. In his study, numbers of Araneae were actually relatively consistent between trees, irrespective of tree species. Also, results from his comparison of the invertebrate diversity in differently aged spruce, showed that younger trees supported a marginally higher proportion of Araneae. If anything one might expect a mature woody habitat to be preferred given the requirement for web-spinning spiders in particular for a complex architecture (Hatley & Macmahon, 1980). Nonetheless, assuming complexity of vegetation is the key to spider numbers and diversity (*e.g.* Docherty & Leather, 1997), the ageing process, although often believed to enhance complexity, may also have a neutral-to-negative effect on woody structural complexity ultimately, particularly where management has been inappropriate (Zenner, 2004).

Maudsley *et al.* (2002) indicated that vegetation at hedge base is actually more important for Araneae in general, than the hedge proper, at least in winter. This study also found that Araneae were more abundant at hedge bottom than in the canopy, although it is unclear to what extent this could be attributed to differences in sampling. Shelter from wind is thought to be an important factor in influencing the abundance of hedgerow spiders, which may be related to hedge orientation and/or vegetation density rather than age or growth stage. Avoidance of the generally more exposed conditions in a hedge canopy might also be expected.

Regarding the seasonal abundance of Araneae, unlike many other arthropods they can remain active all year round, even at low temperatures, provided prey such as Collembola are available (Maudsley *et al.*, 2002). Judging by results in this study, sampling may be just as productive in September as in July, and perhaps even more so. Hsieh & Linsenmair (2012) conducted a year-round survey of arboreal Araneae in beech canopies and found that the months from August to October yielded a higher abundance of spiders than other seasons.

5.4.7. 'Rarity' amongst canopy invertebrates

Far fewer invertebrates and fewer taxa were caught in total in the canopies of the hedgerows compared with the base of the hedgerows. Forestry studies have indicated that there are indeed more invertebrates at ground level than in the canopy (*e.g.* Preisser *et al.*, 1998). Certain taxa were particularly infrequently sampled from the canopies and apparently made up very small percentages of the assemblage (<1%): Lepidoptera, Pulmonata, Opiliones, Dermaptera, Neuroptera, Ispoda, Julida and Polyxenida. There is little published material to help contextualise the abundance of some of these taxa in hedgerows, although moths are reportedly not supported by hedgerows as well as other

AES measures (Fuentes-Montemayor *et al*., 2011a & 2011b). The ecologies of others, for instance myriapods, suggest they are variously cryptic or simply are not usually associated arboreal habitats. Apparent abundance and diversity may be subject to negative 'edge effects' as previously described. Some taxa with more 'arboreal' life cycles would likely be better served by alternative habitat creation such as the creation of woodier habitats - planting of more trees and woodland.

It is difficult to determine the extent to which the impression of rarity of certain taxa is a reflection of genuine distributions or an artifact of sampling. Hedgerows are by no means favoured by all invertebrate taxa, even though they have long been considered invaluable to conserving biodiversity (Pollard *et al*., 1974; Barr *et al*., 1995; Barr *et al*., 2005; Staley *et al*., 2012a). Pollard & Holland (2006) also report rather low incidence of some of these taxa: I made a direct comparison on the basis of % of total assemblage and found that Opiliones, Dermaptera and Neuroptera formed <2%, <1% and <0.5% of total numbers respectively (Appendix A, Fig. A8).

Only a handful of **Isopoda** were found in total, most of these in Mature hedges. Habitats providing numerous crevices and microsites where woodlice can hide, *e.g.* loose bark, tend to be productive (Hopkin, 1991). Mature hedges might therefore be expected to be better suited to the ecological needs of Isopoda, by providing a greater number of places to conceal themselves. Hopkin (1991) indicates that they occur in a wide range of habitats and can be searched for 'almost anywhere', although generally their preference seems to be for damp habitats at ground level, often under stones, leaf and plant litter or rotting wood.

Julida (Diplopoda) were found in very small numbers in the canopy environment and only in Mature hedges. They were caught in 3 hedges only and one hedge accounted for the majority, the same Mature hedge in which the only specimens of Polyxenida were found. Bark, particularly loose old bark, and dead wood can provide suitable dwelling places for Diplopoda (Golovatch & Kime, 2009). Millipedes are however generally regarded as ground-/soil dwellers (Coleman *et al.*, 2004) and are believed to be originally a forest floor-dwelling group (Golovatch & Kime, 2009). Chinery (2007) does however indicate that certain Julida climb trees to browse on algae and mosses. Gruppe *et al.* (2008) suggest that some arthropod taxa normally seen as ground-living, such as Diplopoda and Isopoda and most Opiliones are capable of reaching woodland canopy in "remarkable" numbers, but this seemed not to be the case for hedgerow canopies.

Neuroptera were rarely caught at ground level and also proved elusive at canopy level. Neuroptera are described as largely nocturnal/crepuscular and Plant (1997)

recommends early morning outings as the most productive time for beating. Joyce *et al.* (1997) also indicated low numbers of Neuroptera in the hedge canopy, despite using a fogging technique, and sampling at regular intervals between 6am and 6pm on days during the summer when insects, including lacewings, are often at their most active (Plant, 1994). Like Pollard & Holland (2006), Joyce *et al.* (1997) also found Neuroptera to be present in very low numbers and therefore as a very small proportion of the overall assemblage: Neuroptera formed <1% of the total assemblage, which findings from my study echo, irrespective of differences in sampling.

What reinforces the impression of scarcity is the paucity of information about distributions: Plant (1997) indicated that there were large areas in Britain that were poorly recorded, or indeed not at all. Atlas data and the NBN Gateway reveal gaps in the records, reinforcing the impression of rarity, although under-recording of many taxa, especially in arable farmland, is evident for obvious reasons. Common hawthorn (*Cretaegus monogyna*), the principal hedgerow species, is not given explicitly as a preferred habitat, but deciduous tree species, notably oak (*Quercus robur*) are named (Plant, 1994; 1997). The few Neuroptera that were collected from the hedge canopies in this study were more likely to be found in the Mature hedges, but appeared to be genuinely sparse in farmland hedgerows.

Polyxenida were found only in one mature hedge, tucked beneath some loose bark which broke off and fell into the beating funnel. They seem to be generally cryptic and maybe not easily dislodged from the hedgerow. It is unclear whether they are genuinely rare in the farmed environment, or rather simply hard to get at. Their presence under the bark of a mature hedge might suggest they would be more likely to inhabit mature habitat with well-developed bark than a younger hedge. Therefore, the presence of mature hedges that might even be approaching decrepitude, despite management efforts, would seem to be important for such organisms.

5.4.8. Invertebrate diversity in the hedge canopy

Diversity in the canopy was in general not greatly affected by hedge age type, although there was a significant negative correlation with age for Simpson only. It was unclear why only Simpson should show a relationship with age, but should be noted that results for Berger-Parker and Taxon Richness showed a relationship approaching significance, also negative. This indicated a reduction in diversity as the hedgerow habitat matures and is interesting in the context of studies which demonstrate an ‘ambiguous’ association between invertebrate assemblages and maturity of habitat. Month was

important to all but one measure, Heip. July was the peak month by some measures (notably Taxon Richness), and for others September, likely to be due to an assemblage marked by lower, but more evenly distributed abundance of different taxa. A clear difference in assemblage structure (TADs) of the respective hedge types was shown for September only. There were no obvious reasons why the values of Heip should be unaffected by month by contrast with other measures of diversity, other than to underline again, the sometimes inconsistent nature of responses of different indices to the same conditions.

Data from two canopy studies by Pollard & Holland (2006) and Floren (2008) have been used to generate diversity indices to try to contextualise diversity measures obtained from this study. Pollard & Holland (2006) presented abundance data for 50 taxa consisting of a mixture of families and orders, comprising 11 taxa at Order level, while Floren (2008) presented data for 8 major groupings at Order level (no 'finer grain' inventory). Neither study includes Acari, Collembola or Thysanoptera or Myriapods.

Pollard & Holland's (2006) 50 taxa mixed assemblage achieves a Shannon value of 2.96 and a Simpson value of 11.35, but had the numerically large groups Acari, Collembola and Thysanoptera been included diversity values may well have been lower. At Order level, using the top 11 orders only from the Pollard & Holland (2006) study and my study, diversity values were significantly lower: Shannon diversity was 1.60 in my study compared with 1.74 the study by Pollard & Holland (2006) and Simpson diversity was much reduced at 3.54 (Pollard & Holland, 2006) compared with 4.75 (my study). These relatively modest diversity values might reflect a 'loss of information', which can be a risk in using a higher taxon level approach to characterise invertebrate assemblages (New, 1996). They also serve to illustrate the way in which choice of index is capable of leading to different conclusions about levels of diversity.

In Floren's (2008) forest canopy study the author used broad taxonomic groups at Order level to make an inventory of invertebrates in the canopy of mixed woodland. He compared the assemblages of differently aged woodland: young (8-years-old), intermediate (80-years-old), and old-growth primary. Floren (2008) found that 80-year-old spruce (*Picea abies*) was more diverse than young spruce, but by a seemingly small margin, and the old-growth woodland fell somewhere in between, although it is difficult to know how close in value they really are. Based on the order-level taxonomic groupings, the young spruce averaged Shannon diversity of 1.90 and Simpson diversity of 6.17, whereas the intermediately-aged spruce averaged a Shannon diversity index value of 2.01 and a

Simpson diversity value of 7.47, and primary spruce woodland 1.96 and 5.40 respectively. The oak (*Quercus robur*) trees in primary woodland by contrast had the lowest diversity, compared with younger woodland.

For oak and spruce total numbers of invertebrates were highest in primary woodland and lower in younger, managed woodland, suggesting a successive increase in abundance with maturity, although not an increase that works on relatively short times spans of decades, but over much longer periods of centuries. Assemblage development may take place over much longer time spans than seen in the hedges, which are estimated to be no older than the Enclosures of the $18^{th}/19^{th}$ centuries, with perhaps no truly ancient specimens. This could account for the lack of difference in both abundance and diversity between the Mature and New hedges: the age-span was comparatively small to be able to detect differences in 'colonisation'. It could also mean that planting new hedges leads to relatively rapid acquisition of invertebrate assemblages and therefore represents a 'quick' gain in habitat creation on farmland. Certainly, Munro *et al.* (2009) have found that what they term 'ecological plantings' of woody and herbaceous species for wildlife can achieve similar characteristics (notably structural) of older 'remnant' vegetation within a relatively short time frame of 30-40 years, but may not be comparable at the ground layer. The latter is interesting with regard to differences already noted in the hedgerows at ground level, where there was a significant difference in the diversity of the invertebrate assemblage to maturity of habitat.

5.4.9. The use of broad taxonomic groups in assessing diversity of the canopy

Comparison with other canopy studies such as Pollard & Holland (2006) suggests that the use of order level itself has contributed to a 'damping down' or underplaying of diversity in the invertebrate assemblages. Mature hedgerows did not show superior diversity in the canopy based on the use of broad taxonomic groups. Although there were differences between the taxonomic make-up of the two hedge age groups, also reinforced with further investigation of Coleopteran and Dipteran fauna below the level of Order, these differences were often subtle. Rather than highlighting the inadequacy of a coarser-grain approach to assessing invertebrate biodiversity, this may point to the strong influence of the wider environment and surrounding land use on the assemblages of the hedgerows. Agro-ecosystems, especially arable farmland, have been characterised as impoverished (Biaggini *et al*., 2007).

With regard to other potentially useful reduced-effort approaches to assessing biodiversity, the merits of using a small selection of taxa or even a single taxon (abundance

only) approach were inconclusive. Correlations between taxa showed that several large groups (Collembola, Hemiptera, Hymenoptera) could be capable of acting as proxies for other taxa at a fundamental level, whereby Hymenoptera (dominated by groups such as Chalcidoidea and other Parasitica) showed perhaps the most promise in this respect because of its stronger multiple pairwise correlations. To an extent, this might support Anderson *et al.*'s (2011) view of parasitoid Hymenopteran abundance as a suitable indicator for general invertebrate diversity in certain agricultural habitats. This is not to say Hymenopterans would be a suitable 'surrogate' for all taxa: Lepidoptera were, for instance, not correlated with any other taxon. Correlations with diversity measures were also conducted. Again, relationships tended to shift depending on the month of sampling, so that, for instance, Psocoptera offered themselves as a particularly strong correlate with diversity in September and were the only taxon showing a positive relationship with Taxon Richness, Shannon and Simpson indices.

No single taxon was found to have significant powers of discrimination between the two hedge age types for all months, although different individual taxa were capable of offering some degree of discrimination depending on month of sampling. These findings not only underline the close similarity between the assemblages of hedge age types, but tend to reinforce the notion that use of such indicator taxa as proxies or surrogates for wider diversity may be no better than broader studies of invertebrate assemblages.

5.4.10. Beating as a sampling technique

Beating is a relatively routine method of collecting invertebrates from tall woody vegetation for presence/absence inventories, typically in forest ecosystems (Ozanne, 2005). Versions of the technique have also been used to sample invertebrate populations in hedgerow studies (*e.g.* Ysnel & Canard, 2000; Maudsley *et al.*, 2002; Amy *et al.*, 2015).

Beating seemed capable of yielding an abundance of different organisms, although numbers were in general perhaps rather lower than expected and did not give the impression of hedgerow canopies teeming with invertebrate life. Another principal technique that has been used to sample invertebrate assemblages in hedge canopy environments is chemical fogging or 'knockdown' with short-acting pyrethrins/pyrethroids (Joyce *et al.*, 1997; Pollard & Holland, 2006), a technique which has also essentially been taken on from forest canopy studies. Chemical knockdown reportedly compares favorably with other sampling techniques in terms of its efficacy and is capable of collecting rather higher densities of invertebrates than beating or sweeping for example (Ozanne, 2005).

Using chemical knockdown, Pollard & Holland (2006) found that Hemiptera were the largest component of hedgerow canopy assemblages, making up around 28% in the former study and almost 50% of the total arthropod abundance in the latter study. In my study Hemiptera were the 3rd largest group after Collembola and Coleoptera, accounting for 14% of total abundance. Even removing Acari, Collembola and Thysanoptera from the equation, as Pollard & Holland do in their study, Hemiptera accounted for ~25% of hedgerow canopy fauna, a much lower proportion of the overall assemblage than observed by Pollard & Holland (2006), but close to that of Joyce *et al.* (1997), despite differences in sampling technique.

Research also suggests that abundance of some components of the invertebrate assemblage is low, even using knockdown (*e.g.* Joyce *et al.,* 1997; Pollard & Holland, 2006). The fact that Joyce *et al.* (1997) reported relatively small numbers of certain taxa in farmland hedgerows, namely Dermaptera, Lepidoptera, Neuroptera and Opiliones, is of interest since low numbers of those taxa were also obtained through beating in this study. If chemical knockdown is as effective as assumed for many taxa then this might corroborate a view of certain organisms being genuinely sparsely distributed in hedgerows themselves. Farmland hedgerow canopies probably present a rather harsh habitat for at least some invertebrates, with more exposure to disturbance by factors such as farming activities and weather, compared with a presumably more sheltered environment at hedge bottom. Admittedly, sampling effects can influence the 'apparency' of organisms. Because certain taxa are known to be nocturnally active (*e.g.* Dermaptera, moths, Neuroptera) and invertebrates were collected during daylight hours only, under-sampling related to time of day is also possible. Further targeted sampling, perhaps beating at dawn or dusk and/or modifying the rate and duration of beating could provide answers. This would need to be compared with alternative techniques, *e.g.* suction sampling the efficiency of which is said to compare favourably with knockdown (Maudsley, 2000).

Correlations suggested that invertebrate diversity of the hedgerow canopies decreased with age. This might point to a difficulty with adequate sampling of larger Mature habitats and the possibility that changes in growth form and structure over time cause issues with apparency if not activity-density, or simply may not favour certain components of the invertebrate assemblage.

5.4.11. Conclusion

There appeared to be some effect of maturity on the abundance of invertebrates, but this was confined to only a small number of taxa, with Acari, Hemiptera and Lepidoptera

apparently showing a significant preference for Mature hedges and Pulmonata for New hedges. There were indications of differential preferences amongst families of Coleoptera and Diptera, and major groupings of Hymenoptera. There was however no effect of maturity on the diversity of invertebrate assemblages overall, although there was an effect of month of sampling, which can be explained in large part by seasonality in the lifecycles of different invertebrate taxa. In terms of invertebrate diversity, given that the canopies of relatively young hedges established under AES seemed quickly to acquire the broad characteristics of more mature hedges (≤ 15 years), it seems to be a case of "plant it and they will come". As Clements & Tofts (1992) have pointed out, no single structure is favoured by all taxa: the richer the hedge habitat availability in terms of growth age and form, the more diverse the assemblage. Therefore new plantings as well as Mature hedges have their role to play in enhancing invertebrate diversity. Certainly, examination of Coleopteran and Dipteran families suggested that New hedges have a complementary role to play in providing suitable living conditions for certain canopy-active groups.

Overall, in terms of biodiversity, contrary to expectation, New hedges proved more or less equivalent to established hedgerow habitats in the farmland studied on a like-for-like sampling basis at canopy level if not at ground level. While Mature hedges may be more important to ground-level diversity, indications are that although the new-planting of hedgerows under AES might not be as appropriate for supporting all components of the invertebrate assemblage at ground level, it may be of equivalent importance for a broad range of taxa at canopy – and at different times of year – within an average of 10 years.

Chapter 6. Determinants of hedgerow invertebrate assemblages

6.1. Introduction

Investigations of the effect of habitat maturity on the invertebrate abundance and diversity in hedgerows at ground level and canopy level showed negligible association with age *per se*. Mature hedges appeared to offer preferable conditions to certain taxa and overall showed superior diversity at ground level. The New hedges did show benefits for some taxa but at canopy-level showed no apparent difference in abundance or diversity from Mature hedges. The question remained, therefore, regarding which were the key factors influencing the abundance and diversity of hedgerow invertebrates? Here relationships between faunal abundance and diversity with a number of different abiotic and biotic factors were investigated, the selection of which was informed by general knowledge of the determinants of invertebrate abundance and review of previous studies of invertebrate in hedgerows and other woody habitats. Faunal abundance, taxon richness and diversity were very different in the canopy versus at ground level and the reasons for these differences were also investigated. This part of the investigation was not hypothesis-driven, but rather was a 'data mining' exercise to identify effects on invertebrate assemblages. Such knowledge might inform further study of AES hedges, possibly with manipulations, *e.g.* of habitat variables, such as the botanical composition, height or width of vegetation.

In their review of work on the ecology and conservation status of British hedgerow invertebrates, Maudsley *et al.* (2000) identified a number of key factors affecting the diversity and abundance of invertebrates in hedgerows: botanical composition, structural diversity and shelter, and landscape structure were critical. Corbett & Mole (2005) summarised key factors, for a selection of taxa, corroborating the importance of, for instance, floristic diversity (notably to Heteroptera: Hemiptera) and shelter (notably for butterflies and Carabid beetles).

Pollard *et al.* (1974) and Boatman *et al*. (1994) emphasized the importance of the woody and herbaceous botanical diversity to hedgerow invertebrates and their observations underlined the need for a variety of vegetation to provide for different taxa year round. Forman & Baudry (1984) also indicated the importance of botanical diversity to invertebrates, notably Miridae (Hemiptera). Marshall *et al.* (2001) recorded a positive relationship between the number of plant species present in a site and the diversity of

Heteroptera species. Dover (1996) found that one of the important factors determining abundance and distribution of butterflies in hedgerows was plant species richness. Thomas & Marshall (2000) found a significant correlation between arthropod (notably Carabid beetle) diversity and floral diversity. In addition to the importance of floristic herbaceous diversity to at least some taxa, the idea that the greater the number of woody species, the greater the benefits to wildlife is also long-established (Barr *et al.*, 2005; Natural England, 2008).

The sheltering benefits of hedgerows to a variety of fauna have long been acknowledged. Moore (1968) highlighted the importance to poikilothermic[18] animals of the shelter hedgerows provide from wind and the capability of that shelter to maintain warmer temperatures than open farmland. Numerous authors have identified the sheltering quality of the hedgerow structure, and the terms 'refugia', 'refuge' or plain 'shelter' for wildlife are commonly applied to hedges (*e.g.* Pollard *et al.*, 1974; Dowdeswell, 1987; Maudsley *et al.*, 2000; Hayes *et al*., 2001; Barr *et al.*, 2005; Staley *et al.*, 2013; Hedgelink, no date d). Shelter may however be less important to some taxa than others: for instance, Dover (1996) found that butterflies benefited from the shelter of hedgerows and Maudsley *et al.* (2002) showed that wider hedges were more beneficial for Staphylinid beetles, but also found no significant relationship between hedge width and Carabid beetle and spider abundance in the hedge base. Pywell *et al.* (2005) also emphasized the sheltering effect of hedgerows, specifically for overwintering predatory invertebrates in the hedge bottom, where vegetation height was associated with hedge age. The effect of sward characteristics, such as height, on the abundance and diversity of invertebrate populations at ground level in the hedge base and margin/protection zone, are important factors to consider (Asteraki *et al.*, 1995; Vickery *et al.*, 2009). Maudsley *et al.* (2002) indicated that there was some evidence that shelter from wind is an important factor influencing the abundance of spiders in the hedgerow itself, which might be determined by prevailing wind direction and/or density of foliage.

Regarding hedge-base invertebrates, leaf litter has been found to correlate positively with, for example, predatory beetle groups (Maudsley *et al.*, 2002) and is widely recognised as an important factor in the ecologies of many invertebrates on the ground and in the soil (*e.g.* Pollard *et al*., 1974; Coleman *et al*., 2004). Amy *et al.* (2015) found that

[18] Regulating body temperature by behavioural means, such as basking or burrowing (Allen, 1985). All insects are considered to be poikilotherms in that their body temperature varies with that of surroundings, and their basic metabolism is dependent on ambient temperature (Speight *et al.*, 1999).

foliage biomass in the hedge top had a positive effect on the abundance of herbivorous and predatory invertebrates. Although neither leaf litter at ground level nor foliage biomass of the canopy were measured directly in my study, the dimensions and a measure of density of ground- and canopy vegetation were included and could be treated as a proxy measure. Leaf litter was a common ecological requirement for many of the taxa that thrive at ground level, including groups that were found in greater abundance in Mature hedge bottoms (see Chapter 4).

Other researchers have emphasized the importance of the 'landscape context' of hedgerows, such as hedgerow network connectivity/connectedness and distance from woodland habitat, as determinants of invertebrate populations, notably Carabid beetles, spiders and butterflies (*e.g.* Burel & Baudry, 1994; Gruttke & Kornacker, 1995; Petit & Usher, 1998; Barr *et al.*, 2005; Burel & Baudry, 2012; Fischer *et al.*, 2013). Both connectivity and distance from woodland were included in modelling of effects on the broad assemblage of invertebrates in my study. Landscape-scale biodiversity conservation which might eventually include having farmers collaborate on AES options, such as coordinating hedgerow creation and management, has recently been put forward as a means of making better progress in preserving and enhancing biodiversity in the farmed environment (McKenzie *et al*., 2013).

Climatic factors and weather conditions, which are also considered below, are well-known to influence the ecologies of insects and other invertebrates (Speight *et al*., 1999), such that their influence on hedgerow fauna is probably taken for granted. Nonetheless, weather is worth inclusion in modelling of effects on invertebrate assemblages, since all taxa do not necessarily respond to weather conditions in the same manner. An examination of the influence of weather on distributions of hedgerow invertebrates is also warranted, given the value of hedgerows as shelter. The amount of shelter a hedgerow can provide may be important in the face of disturbance, not only by agricultural land use but by weather which, according to some commentators, may become increasingly unpredictable and extreme (Mossman *et al*., 2013).

Management, although not considered directly in my study, contributes directly and indirectly to the quality of hedgerow habitats, for instance, their structure and value as shelter) for invertebrates and other wildlife. Its importance has been considered many times, ultimately informing agri-environmental policy, prescriptions and advice to farmers (Pollard *et al*., 1974; Dowdeswell, 1987; Maclean, 1992, 2003, 2006; Barr *et al.*, 2005 and Staley *et al*., 2012b). Along with cutting frequency and timing, other traditional

management techniques, such as coppicing and laying, continue to be promoted as beneficial for hedgerow fauna. McAdam *et al.* (1994) demonstrated the benefits of laying in creating denser hedgerow structures beneficial to a wide range of insect fauna. More recently research has re-visited AES cutting regimes and how this affects hedgerow structure and botanical diversity for a wide range of wildlife including invertebrates (*e.g.* Staley *et al.*, 2012b). After data were scaled to account for hedge height, unmanaged controls supported more herbivores and predators than all treatments barring an experimental, mechanised form of wildlife hedging which incorporated a form of laying and retention of brash (Amy *et al*., 2015). Although cutting regime is deemed important, continued focus of AES funds on this aspect of management at the expense of rejuvenation activities is regarded as detrimental to hedge health by those tasked with hedgerow conservation. Indeed, Hedgelink (2014) have called for a move away from reliance on cutting regimes to improve farmland hedgerow condition, and thereby biodiversity value, and emphasized the need for more investment not only in rejuvenation measures such as coppicing, laying, gapping up, but also planting. AES monies for the rejuvenation of farmland hedgerows plummeted under AES payment schemes in the last decade and are now deemed to be the preserve of Higher Level Stewardship farms only, rather than retaining their rightful place as a fundamental Entry Level option (Wolton, 2011). Revised Countryside Stewardship agreements with options and grants for cutting, hedge-laying and planting are addressing this deficit (Natural England, 2015).

Information on hedgerow cutting/management regimes undertaken by the land managers on farms visited in this study was variable, in some cases limited. Insufficient evidence of recent rejuvenation attempts in the Mature hedgerows in my study to include as workable categories for modelling, although most bore the signs of historic laying and in one or two evidence of old coppicing could be seen. Many of the New hedgerows contained some trees suitable for coppicing, *e.g.* hazel (*Corylus avellana*) and field maple (*Acer campestre*), but which had been left to grow. At one farm a number of New hedges had been laid. One of the Mature hedgerows included in the study, but none of the New hedges, were cut during the sampling period.

The categories investigated below are: botanical composition, structure of ground vegetation at hedge base, structural attributes of the woody hedgerow itself, landscape context and weather. The following section defines the variables included in the modelling and the modelling technique itself in more detail. This chapter will show the use of multivariate analysis on ecological data, specifically the abundance and diversity of

hedgerow invertebrates collected at ground level (by sticky trap) and canopy level (by beating). While many of the factors have been tested before on this or that taxon (notably predatory arthropods such as Carabid beetles and spiders) such as Maudsley *et al.* (2002), this study looks at a broader spectrum of invertebrate taxa.

6.2. Methods

6.2.1. Collected variables

The variables recorded were based on the requirements of the Hedgerow Survey Handbook (Defra, 2007) and/or habitat and other variables investigated in research, such as that by Maudsley *et al*. (2002), on the overwintering predatory arthropods of a single hedgerow. Not all data collected on variables are included in the modelling. Prior selection of variables was conducted using Spearman's correlations and auto-correlated determinants were excluded. For instances botanical diversity of the margin 'swathe' taking into account the full margin width was found to be significantly correlated with botanical diversity measured by the 2 x 1m quadrat.

The selected factors were used in multivariate analysis based on models using Akaike's information criterion to determine key factors in explaining hedgerow invertebrate abundance and diversity. Methods of collection of this data are described in Chapter 3, but briefly summarised here under a broad heading:

- **Botanical diversity** – measured by taxon richness of woody and grassy vegetation both in the hedgerow and at the hedge base as measured using a 2m x 1m quadrat (as used in the Hedgerow Handbook survey methodology) and immediately around the trap site within a 25cm radius;
- **Ground vegetation structure (hedge bottom)** – ground cover, sward height, ground light (as a measure of vegetation density in the hedge base);
- **Hedge structure (woody hedgerow proper)** – height, height growth during sampling, canopy width, width growth, canopy light (as a measure of ca**nopy vegetation density);**
- **Landscape context** – location, connectivity, distance from woodland;
- **Weather** - humidity, rainfall, temperature, wind speed.

Abbreviations are used for the variables throughout the results section and are given in Table 6.1 below.

Table 6.1. Abbreviations and definitions of biotic and abiotic variables used in statistical analysis explaining hedgerow invertebrate abundance and diversity

Definitions of Explanatory variables	
Botanical diversity:	
WTR	Woody Taxon Richness = number of tree/shrub species in 30m survey transect.
MVTRQ	Margin Vegetation Taxon Richness Quadrat = Botanical/vegetation taxon richness in the margin as measured in the 2m x 1m survey quadrat.
TVTR	Trap Vegetation Taxon Richness = number of botanical/vegetation families in immediate vicinity of the sticky traps at ground level (within ≤ 25cm radius of trap).
Ground vegetation structure:	
CQ	Cover Quadrat = a visual estimate of the amount of bare ground as measured in the 2m x 1m survey quadrat.
GL	Ground Light = the light penetration at ground level measured using a luxmeter and calculated as a % from the difference between measurements of light at hedge base and ambient light. A measure of vegetation density.
MSH	Maximum Sward Height = the height of the tallest herbaceous vegetation in the hedgerow protection zone.
MW	Margin Width = width of the hedge base/protection zone, measured in cm from the centre of the hedgerow.
Hedge structure:	
CL	Canopy Light = the light penetration in the canopy measured using a luxmeter and calculated as a % from the difference between measurements of light in the canopy and ambient light.
COA	Canopy Overhang = width of canopy overhanging the hedge bottom.
HA	Height August = height of hedgerow measured in cm to the nearest 25cm.
HAA	Height Above Ground August = the distance between the bottom edge of the canopy and the ground in cm.
HG	Height Growth = growth of hedgerow height between start of surveying in March and end of survey in August.
WG	Width Growth = growth of hedgerow width between start of surveying in March and end of survey in August.
Landscape context:	
C	Connectivity/connectedness = number of hedgerows with which individual hedge is connected (with a distance of ≤ 20m between hedges).
DW	Distance from Woodland = measured from the centre of the hedgerow to the edge of the nearest woodland as the crow flies using Ordnance Survey (OS) maps.
L	Location = Nettleham, Potterhanworth, Riseholme, Swallow
Weather:	
R	Rainfall = rainfall (mm) from Wunderground for sticky trapping at hedge bottom averaged over the 4 day trapping period; no rainfall taken measured for the canopy beatings since beating never conducted in wet weather.
H	Humidity = humidity (%) from Wunderground for sticky trapping at hedge bottom averaged over the 4 day trapping period. Humidity was measured as a snapshot during the beatings using a handheld Silva weather station.
T	Temperature = temperature (^{0}C) from Wunderground.com for sticky trapping at hedge bottom averaged over the 4 day trapping period. Temperature was measured as a snapshot during the beatings using a handheld Silva weather station.
W	Wind speed = wind speed (km/h) from Wunderground for sticky trapping at hedge bottom averaged over the 4 day trapping period. Wind speed was measured as a snapshot during the beatings using a handheld Silva weather station.

All data were collected within the 30m transect, unless indicated otherwise. Further information on how these variables were collected/calculated can be found in Chapter 3.

6.2.2. Statistical analysis

Chapter 3 provided some general background to the statistical testing employed in my study, but the multivariate technique used to explore determinants of hedgerow invertebrate abundance and diversity is described here in further detail. A modelling technique based on Akaike's information criterion (AIC) was used to determine which variables were best at explaining the abundance and diversity of invertebrates found in the hedgerows sampled. In fact a modified version of AIC was used, *i.e.* AICc, which is Akaike's corrected Information Criterion (Cavanaugh, 2012), as recommended by Symonds & Moussalli (2010) for small sample sizes[19]. The statistical package R (version 2.15.3) was used to extract AIC values from the outputs of generalised linear models (with Poisson distribution) for input into the Akaike modelling. The Akaike modelling was conducted using Microsoft Excel. AICc values were calculated from the AIC values, taking into account the number of samples and number of model parameters. Modelling and ranking of the models took place using Excel.

Use of AIC/AICc in analyses is increasing in popularity in the field of ecology (Symonds & Moussalli, 2010). It enables a comparison and ranking of multiple competing models which have been used to investigate the factors underlying any biological phenomenon, from which a best approximation of the factor(s) determining results can be derived. The method produces values which are not intrinsically interpretable, that is to say it is not meaningful to talk about AIC and AICc values being large or small *per se*, but are useful for comparing models (Field, 2009). Smaller AIC values mean better fitting models (Field, 2009; Symonds & Moussalli, 2010). The presentation of the outcomes of Akaike modelling follows that of Kervinen *et al.* (2012) whereby:

- k = the number of perameters used in the modelling, including intercept;
- AICc = Akaike's corrected Information Criterion, usually for smaller sample sizes ($\leq$40) but can be used as a default also for larger sample sizes;
- Δ_i = the difference between the AIC value of the best model and the AIC value for each of the other models to show how a model compares to the best model;

[19] Symonds & Moussalli (2010) also point out that use of AICc as a default is often advised even with large sample sizes

- w_i = the Akaike weight, calculated from Δ_i above. Akaike weights range between 0 and 1, with the sum of Akaike weights of all models in the candidate set being 1. Although a best available model(s) can be determined from this process, models do not show significance of effects *per se*. The Akaike weight of the models can nonetheless be treated as "analogous to the probability that a given model is the best approximating model" (Symonds & Moussalli, 2010). Thus, for example, if the best model has a w_i of 0.49, this can be interpreted to mean that there is a 49% chance that it really is the best approximating model describing the data among the candidate models;
- acc w_i = cumulative sum of the Akaike weights for each model in which a variable appears. Can be used as a measure of the relative importance of models under consideration;
- ER = the evidence ratio, calculated using Δ_i. The evidence ratio number will indicate how many times more likely the first and best model is than the second, third and all following models.

Explanatory variables were modelled according to broad categories (as described above) rather than creating a 'maximal' model into which all variables were input. This was done in order to control the number of tests conducted at any one time on the dataset. Main effects only were tested, in order to try to control the number of tests required. Interactions could be added with the risk of increasing the difficulty of interpretation.

Models were ranked based on AICc values. Not all models generated by the analysis were included in the presentation tables, in the interest of parsimony. Symonds & Moussalli (2010) suggest that only those models with Δ_i values less than 2 should be retained since they are essentially as good as the best model, and that is the protocol followed here. There is however a lack of consensus on when a model can be rejected: Kervinen *et al.* (2012), for instance, used a cut-off point of 3, with some authors suggesting retention of models with Δ_i values up to 6 (Richards, 2005) or even 10 (Burnham & Anderson, 2002).

Symonds & Moussali (2010) describe how Akaike model weights (w_i) can be used to estimate the relative importance of individual variables under consideration. In order to do this, Akaike weights are summed for each model in which a particular variable appears, with the highest value indicating the best determinant. If an explanatory variable appears in the top models, its summed Akaike weight will tend towards 1, whereas if it appears in

models lower down the rankings it will tend more towards 0 (Symonds & Moussalli, 2010). The summed weighting of the respective variables can be interpreted as an equivalent to the probability that they are (relatively) more or less important components. This method of identifying key determinants of ecological phenomena was applied to my hedgerow invertebrate data. Summed AIC weights (w_i) for all modelled variables have been used to generate 3D column charts, which help visualise the relative importance of explanatory factors in determining the invertebrate abundance and diversity of both hedge top and hedge bottom.

Additionally, descriptive data on the averaged Akaike weights for each individual variable in relation to both invertebrate abundance and diversity, at both ground- and canopy level are presented (Akaike mean & median weights, ±SD and ±SE). Averaged Akaike weights for all explanatory variables were also tested using Kruskal-Wallis to evaluate whether there was any significant difference between the weightings of the individual model components. Mann-Whitney U was used to perform *post hoc* tests on the Kruskal-Wallis results, where the outcome showed a significant difference between the individual variables. This in turn indicated which individual variables might provide a significant explanation for patterns of invertebrate abundance and diversity. Spearman's rank correlations (with B-Y FDR corrections for multiple comparisons) were subsequently conducted on the variables identified by *post hoc* tests to determine the strength of the relationship between those variables and invertebrate abundance and diversity at both hedge canopy and ground level.

6.3. Results

6.3.1. Botanical diversity – effects on invertebrate abundance and diversity

A total of 22 botanical families plus the Division Bryophyta (Mosses) were found in the hedge bottoms (Appendix D, Table D1). Botanical diversity at ground level (also in hedgeless boundaries) was dominated by: Poaceae (Grasses); Apiaceae (Carrot Family), notably *Anthriscus sylvestris* (Cow Parsley) and *Heraclium sphondylium* (Hogweed); Convolvulaceae (Bindweed Family), notably *Calystegia sepium* (Hedge Bindweed) but also *Convolvulus arvensis* (Field Bindweed); Rubiaceae (Bedstraw Family), notably *Galium aparine* (Cleavers); and Urticaceae, notably *Urtica dioica* (Stinging Nettle).

The average number of botanical families in the vicinity of the trap site (TVTR) per hedge bottom for all months combined (n = 95) was 6. There was a significant difference between the botanical diversity (Taxon Richness in the immediate vicinity of the trap locations) of the bottoms of Mature hedges (n = 48) versus New hedges (n = 47) for all

months combined (April, July and September), whereby Mature hedges were significantly more botanically diverse: mean = 6 (±SD 1.68) versus 5 (±SD 1.66) taxa (Mann-Whitney $U = 868.50$, $n_1 = 48$, $n_2 = 47$, $p = 0.049$).

A survey of the taxon richness (family) of ground vegetation in the hedge bottom was undertaken once in July using a quadrat (MVTRQ). On average, for all hedges combined (n = 32), there were 7 (±SD 1.78) botanical taxa per hedge using this method. No significant difference between the botanical taxon richness of Mature hedge bottoms (n = 16) versus New hedges (n = 16) was shown (Mann-Whitney $U = 89.00$, $n_1 = 16$, $n_2 = 16$, $p = 0.133$).

A total of 11 woody/shrubby species were counted in the hedgerow survey transects. Woody botanical diversity was dominated by *Crataegus monogyna* (Common Hawthorn) overall. Some Mature hedges had been planted historically with *Fraxinus excelsior* (Ash) and/or had acquired species such as *Sambucus nigra* (Elder) and *Prunus spinosa* (Blackthorn), *Rosa canina* (Dog-rose) and *Rubus fruticosus* (Bramble) over time. New hedges tended to have been planted with a little more variety, notably *Acer campestre* (Field Maple), *Corylus avellana* (Hazel), in addition to blackthorn, with a limited number of more 'unusual' components such as *Cornus sanguinea* (Dogwood), *Euonymus europaeus* (Spindle) and *Viburnum opulus* (Guelder-rose). On average hedgerows (n = 32) had a woody taxon richness (WTR) of 3 species (±SD 1.78). There was no significant difference between the woody diversity of Mature hedges (n = 16) versus New hedges (n = 16) (Mann-Whitney $U = 127.00$, $n_1 = 16$, $n_2 = 16$, $p = 0.969$).

6.3.1.i. Invertebrate abundance

Woody taxon richness (WTR) and the measure of botanical taxon richness around the trap site (TVTR) were the components of the top model explaining the abundance of all ground-active invertebrates combined (Table 6.2). It was however TVTR and not WTR that was a prominent factor in models explaining the abundance of invertebrate groups at ground level overall (Appendix D, Table D2 and Fig. 6.1a). In fact, TVTR contributed to all 3 top models explaining the total abundance of all taxa at ground level. It also contributed to more top ($\Delta i \leq 2$) model fits for individual taxa than either botanical taxon richness of the hedge bottom measured by quadrat (MVTRQ) or the woody/shrubby taxon richness of the hedgerow itself (WTR) (Appendix D, Table D2). Only in the case of Diptera did TVTR not contribute to the top models, in which case WTR was the most important factor.

TVTR was also the most prominent component of top models explaining the abundance of invertebrates at canopy level, with the exception of Psocoptera (Table 6.2, Figs. 6.1b and Appendix D, Table D3). It should be noted that for a number of individual taxa, particularly at canopy level, the value for intercept only ranked ahead of any explanatory models, indicating that the variables selected, even woody diversity, did not provide a robust explanation of invertebrate presence in the hedge tops.

Figure 6.1 illustrates the rather mixed picture regarding the importance of botanical diversity to taxonomic abundance in explanatory models, but do help visualise the comparatively large contribution made by TVTR to models for both ground level and canopy level. TVTR had the highest mean Akaike weighting for invertebrate abundance generally at both ground- and canopy-level (Table 6.3). The Akaike weights (w_i) suggested that in no case was there more than a 50% probability that the models represented the best explanation for abundance, which points to the influence of other factors.

Only in the case of canopy-level invertebrate abundance was there a significant difference between the explanatory power of these model components, with Kruskal-Wallis and *post hoc* Mann-Whitney *U* tests indicating TVTR to be a significantly more important contributor to taxonomic abundance overall than either WTR or MVTRQ (Table 6.3 & Table 6.4). Hence, for the canopy-active invertebrates only, a Spearman's rank correlation between TVTR and the abundance of individual taxa indicated that three of the 10 individual taxa showed a significant but rather weak positive relationships with moderate to small coefficients: Acari (r_s = 0.322, p = 0.003, Thysanoptera (r_s = 0.352, p = 0.001), Lepidoptera (r_s = 0.338, p = 0.002). For the remaining taxa, there was a very weak non-significant relationship between canopy-active invertebrate abundance and TVTR, both Araneae and Psocoptera showing virtually nil response to botanical diversity (Appendix D, Table D4).

6.3.1.ii. Invertebrate diversity

For all measures of diversity at ground level, the intercept-only appeared above the ranked models, indicating that the explanatory variables selected on their own did not form particularly compelling explanations for invertebrate diversity (Table 6.5a). Despite its apparent importance to invertebrate abundance at canopy level, there was not such a prominent influence of TVTR on measures of invertebrate diversity in the canopy. TVTR on its own was the top model for taxon richness only and WTR for Heip only (Table 6.5b).

For invertebrate diversity at ground level the highest mean AICc weighting (all models) was for MVTRQ (richness of margin vegetation) and at canopy level TVTR (trap vegetation taxon richness) (Table 6.6). Model components were overall relatively low and uniform in value at both ground- and canopy level (Table 6.6 and Appendix D, Fig. D1 (a) & (b)). Kruskal-Wallis tests were performed on the mean full-model Akaike weightings of the measures of botanical diversity, but results from the analysis showed no significant differences between the average Akaike model weightings for the respective explanatory variables: at ground level in the hedge bottom, $H = 4.34$, $p = 0.114$; at canopy level in the hedge top, $H = 0.88$, $p = 0.645$. Therefore no especially strongly weighted measure of botanical diversity could be identified to explain overall invertebrate diversity at either ground- or canopy level.

6.3.2. Ground vegetation structure – effects on invertebrate abundance and diversity

Ground cover (CQ) measured within the quadrat (2m x 1m) was estimated as proportion of bare earth and given a Domin score (1-10). This was measured only once during the July vegetation survey. The mean Domin score per hedge (n = 32) was 4.83 (±SD 2.30) which equates to an average of between 11% and 25% bare earth, or conversely between 75% and 89% vegetation coverage. There was no significant difference between the ground cover of Mature (n = 16) and New (n = 16) hedges (Mann-Whitney $U = 94.00$, $n_1 = 16$, $n_2 = 16$, $p = 0.197$).

Ground Light (GL) reflected the amount of visible light (measured in Lux) which reached the trap positions at ground level and differed between months, being far lower in July (peak season for vegetation growth) than either April or September: April = 16.97% (±SD 15.13); July = 7.44% (±SD 6.67); September = 17.58% (±SD 11.48). There was no significant difference between the GL conditions of Mature (n = 48) versus New (n = 47) hedges for all months combined (Mann-Whitney $U = 1093.00$, $n_1 = 48$ $n_2 = 47$, $p = 0.794$).

The Maximum Sward Height (MSH) differed between months: in April (n = 32) the mean was 62.03 cm (±SE 4.57, ±SD 25.84); in July (n = 32) the mean was 115.63 cm (±SE 6.20, ±SD 35.10); in September (n = 31) the mean was 88.71 (±SE 5.18, ±SD 28.84). Overall there was no significant difference between the MSH of Mature (n = 48) versus New hedges (n = 47) for all months combined (Mann-Whitney $U = 1107.00$, $n_1 = 48$, $n_2 = 47$, $p = 0.875$).

The mean Margin Width (MW) for all hedges combined (n = 32) was 3.62 cm (±SD 1.75). There was no significant difference between Mature (n = 16) and New (n = 16) hedges (Mann-Whitney $U = 124.00$, $n_1 = 16$, $n_2 = 16$, $p = 0.880$).

Table 6.2. Best models ($\Delta i \leq 2$) predicting the abundance of invertebrate taxa in hedgerows at ground level (upper table) and canopy level (lower table), using measures of botanical diversity as explanatory variables. Explanatory variables: WTR = Woody taxon richness in the hedgerow itself; MVTRQ = Botanical taxon richness in the margin; TVTR = taxon richness of vegetation in immediate vicinity of trap. Total abundance (all taxa) only shown

Ground level						
Candidate models	**k**	**AICc**	**Δi**	**w_i**	**acc w_i**	**ER**
Total (all taxa)						
WTR + TVTR	3	587.86	0.00	0.49	0.49	---
TVTR	2	589.23	1.37	0.25	0.73	1.98
WTR + MVTRQ + TVTR	4	589.94	2.08	0.17	0.90	2.83
Canopy level						
Candidate models	**k**	**AICc**	**Δi**	**w_i**	**acc w_i**	**ER**
Total (all taxa)						
TVTR	2	463.95	0.00	0.41	0.41	---
WTR + TVTR	3	465.60	1.65	0.18	0.60	2.29
MVTRQ + TVTR	3	465.80	1.85	0.16	0.76	2.53

Table 6.3. Comparison of the averaged full-model Akaike weightings for each measure of botanical diversity used as explanatory variables for invertebrate abundance (all taxa and top 10 individual taxa) at hedge bottom and canopy level. Values for mean, median, ±SD and ±SE are shown

Analysis - explanatory variables		**Akaike Mean (n = 11)**	**Akaike Median (n = 11)**	**±SD**	**±SE**
Ground level	**Invertebrate abundance**				
(Sticky traps)	Woody Taxon Richness	0.566	0.515	0.196	0.062
	Margin Vegetation Taxon Richness (Quadrat)	0.467	0.437	0.151	0.048
	Trap Vegetation Taxon Richness	0.606	0.542	0.292	0.092
Canopy level	**Invertebrate abundance**				
(Beating)	Woody Taxon Richness	0.319	0.290	0.110	0.035
	Margin Vegetation Taxon Richness (Quadrat)	0.428	0.343	0.239	0.075
	Trap Vegetation Taxon Richness	0.596	0.500	0.310	0.098

Table 6.4. Results of Kruskal-Wallis tests (*H*) on differences between the mean full-model Akaike weightings of measures of botanical diversity as candidate explanatory variables for overall abundance of hedgerow invertebrates at ground- and canopy level and of the top 10 most abundant taxa. Post hoc Mann-Whitney *U* tests show comparisons between paired variables. Significant results are highlighted in bold. Asterisk indicates the more highly weighted variable

Analysis - dependent variables		**Kruskal-Wallis**				**Post hoc tests**		
		n	**df**	***H***	***p***	***U***	***p***	
Sticky traps (Ground level)	**Taxonomic Abundance**	11	2	2.59	0.274		ns	
Beatings (Canopy level)	**Taxonomic Abundance**	**11**	**2**	**6.06**	**0.048**	**26.00**	**0.023**	**WTR v TVTR***

Table 6.5a. Best models ($\Delta i \leq 2$) predicting diversity (Taxon Richness, Berger-Parker, Shannon diversity, Simpson diversity, Heip, Simpson evenness) of invertebrate taxa in hedgerows at ground level using measures of botanical diversity as explanatory variables. Explanatory variables: WTR = Woody taxon richness in the hedgerow itself; MVTRQ = Botanical taxon richness in the margin; TVTR = taxon richness of vegetation in immediate vicinity of trap

Candidate models	k	AICc	Δi	w_i	acc w_i	ER
Taxon Richness						
Intercept	1	23.01	0.00	0.38	0.38	---
TVTR	2	24.79	1.78	0.15	0.53	2.43
WTR	2	24.90	1.89	0.15	0.68	2.57
MVTRQ	2	24.97	1.96	0.14	0.82	2.66
Berger-Parker						
Intercept	1	42.25	0.00	0.33	0.33	---
MVTRQ	2	43.17	0.92	0.21	0.53	1.58
TVTR	2	44.13	1.88	0.13	0.66	2.56
Shannon						
Intercept	1	15.01	0.00	0.40	0.40	---
MVTRQ	2	16.99	1.98	0.15	0.55	2.69
Simpson (Diversity)						
Intercept	1	77.55	0.00	0.33	0.33	---
MVTRQ	2	78.60	1.05	0.19	0.52	1.69
TVTR	2	79.29	1.74	0.14	0.66	2.38
WTR	2	79.53	1.98	0.12	0.78	2.69
HEIP (Evenness)						
Intercept	1	12.23	0.00	0.40	0.40	---
MVTRQ	2	14.16	1.93	0.15	0.55	2.62
Simpson (Evenness)						
Intercept	1	11.53	0.00	0.40	0.40	---
MVTRQ	2	13.48	1.95	0.15	0.55	2.65

Table 6.5b. Best models ($\Delta i \leq 2$) predicting diversity (Taxon Richness, Berger-Parker, Shannon diversity, Simpson diversity, Heip, Simpson evenness) of invertebrate taxa in hedgerows at canopy level using measures of botanical diversity as explanatory variables. Explanatory variables: WTR = Woody taxon richness; MVTRQ = Botanical taxon richness in the margin (quadrat); TVTR = taxon richness of vegetation in vicinity of trap

Candidate models	k	AICc	Δi	w_i	acc w_i	ER
Taxon Richness						
TVTR	2	55.71	0.00	0.35	0.35	---
Intercept	1	57.03	1.32	0.18	0.53	1.93
MVTRQ + TVTR	3	57.33	1.62	0.15	0.68	2.25
Berger-Parker						
Intercept	1	37.32	0.00	0.29	0.29	---
WTR	2	37.90	0.58	0.21	0.50	1.34
TVTR	2	38.72	1.40	0.14	0.64	2.01
MVTRQ	2	39.32	2.00	0.10	0.75	2.72
Shannon						
Intercept	1	10.92	0.00	0.40	0.40	---
TVTR	2	12.87	1.95	0.15	0.55	2.65
WTR	2	12.92	2.00	0.15	0.69	2.72
Simpson (Diversity)						
Intercept	1	80.29	0.00	0.25	0.25	---
WTR	2	80.31	0.02	0.24	0.49	1.01
MVTRQ	2	81.62	1.33	0.13	0.61	1.95
WTR + MVTRQ	3	81.70	1.41	0.12	0.74	2.03
HEIP (Evenness)						
WTR	2	13.64	0.00	0.24	0.24	---
MVTRQ	2	13.81	0.17	0.22	0.47	1.09
TVTR	2	13.81	0.17	0.22	0.69	1.09
Simpson (Evenness)						
Intercept	1	18.82	0.00	0.37	0.37	---
TVTR	2	20.63	1.81	0.15	0.52	2.47
WTR	2	20.64	1.82	0.15	0.67	2.49

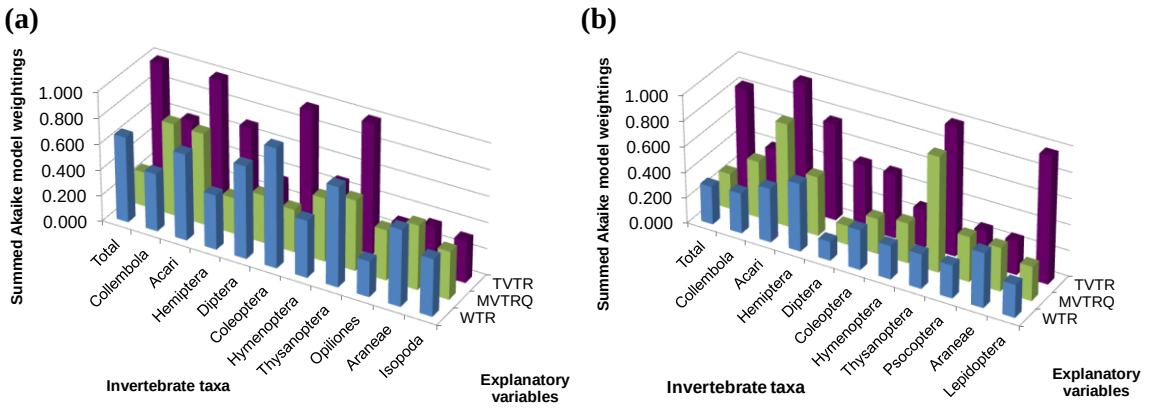


Figure 6.1a-b. Summed candidate Akaike model weights for botanical diversity variables potentially explaining invertebrate abundance at: (a) ground level, and (b) canopy level. Top 10 most abundant taxa only are shown for hedge bottom and hedge top respectively, as well as Total abundance (all taxa). Key to explanatory variables: WTR = Woody taxon richness in the hedgerow itself; MVTRQ = Botanical taxon richness in the margin; TVTR = taxon richness of vegetation in immediate vicinity of trap

Table 6.6. Comparison of the averaged full-model Akaike weightings for each measure of botanical diversity used as explanatory variables for invertebrate diversity (Taxon Richness, Berger-Parker, Shannon diversity, Simpson diversity, Heip, Simpson evenness) at both ground- and canopy level. Values for mean, median, ±SD and ±SE are shown

Analysis - explanatory variables		Akaike Mean (n = 6)	Akaike Median (n = 6)	±SD	±SE
Ground level	**Invertebrate diversity**				
(Sticky traps)	Woody Taxon Richness	0.265	0.263	0.010	0.000
	Margin Vegetation Taxon Richness (Quadrat)	0.303	0.272	0.050	0.020
	Trap Vegetation Taxon Richness	0.271	0.268	0.010	0.000
Canopy level	**Invertebrate diversity**				
(Beating)	Woody Taxon Richness	0.358	0.350	0.100	0.040
	Margin Vegetation Taxon Richness (Quadrat)	0.306	0.281	0.060	0.020
	Trap Vegetation Taxon Richness	0.371	0.304	0.160	0.060

6.3.2.i. Invertebrate abundance

At ground level all four variables describing aspects of structure of ground vegetation made contributions to the top models explaining total invertebrate abundance and abundance of the top 10 most abundant taxa. Maximum Sward Height (MSH) and Ground Light conditions (GL), as a measure of density of vegetation, made more prominent contributions than either ground cover (CQ) or margin width (MW) (Table 6.7; Fig. 6.2a; Appendix D, Table D5). MSH was a component of the top model for 9 out of the 10 most abundant taxa and total invertebrate abundance. Even though MSH and GL were components of the top model explaining total invertebrate abundance, the w_i value

indicated only a 25% probability that this was the best explanatory model among the candidate models for this group (vegetation structure at ground level). There were a range of w_i values for individual taxa, but no model including structural factors of ground vegetation had a better than 50% probability of being the best explanation for abundance. Only in the case of Opiliones was this more than 40% and for the combination of MSH and CQ (measure of bare ground) (Appendix D, Table D5).

Averaged model weightings for invertebrate abundance at ground level showed that MSH was overall the explanatory factor with the highest value (Table 6.8), but Kruskal-Wallis (*H*) tests showed no significant difference in weightings between the 4 model components explaining invertebrate abundance at the hedge base (Table 6.9). Therefore no further exploration of the data using correlations was conducted.

At canopy level, Ground Light (GL) was the most prominent of the factors selected to explain the abundance of invertebrates at canopy level (Table 6.7). GL featured in both top models for total abundance and was the best model or a component of the best model for most of the individual taxa, with the exception of Psocoptera, for which maximum sward height (MSH) was most important, and Lepidoptera, for which no individual factor or model performed better than Intercept (see also Appendix D , Table D6). The 4 selected structural variables provided an indifferent explanatory model for the low numbers of Lepidoptera (Fig. 6.2b). Again, there were a range of w_i values for individual taxa, but no model including structural factors of ground vegetation had a better than 50% probability of being the best explanation for abundance. In the case of Hemiptera and Thysanoptera, however, MSH and GL, plus ground cover (CQ) provided models approaching that (Appendix D, Table D6). Ground Light was the most heavily-weighted of the averaged model components relating to abundance of canopy invertebrates (Table 6.8; Fig. 6.2(b)). Kruskal-Wallis testing indicated that GL was significantly more important than other variables selected in explaining canopy-level invertebrate abundance (Table 6.9).

Spearman's rank correlations between GL and abundance of invertebrates from the hedge top showed that the total abundance of all canopy taxa had a significant negative relationship with ground light conditions (r_s = -0.496, p = <0.001), indicating that as levels of light at ground level increased (with increasingly sparse vegetation) so numbers of invertebrates decreased (and *vice versa*). The negative relationship between GL and invertebrate numbers at canopy level was true for all individual taxa to a greater or lesser extent, and the relationship was significant to highly significant for 7 individual taxa, but not for Araneae, Psocoptera or Lepidoptera (Table 6.10).

6.3.2.ii. Invertebrate diversity

Maximum Sward Height (MSH) was overall the 'top' component explaining invertebrate diversity at ground level, as indicated by the list of best models (Table 6.11a), but only in the cases of Berger-Parker and Simpson (diversity) was MSH ranked above the Intercept-only model. In addition, w_i values indicated that even for the top models there was a 30% or lower probability of these being the best explanatory factors. Summed Akaike values for structural variables explaining diversity of hedge bottom invertebrates were on the whole rather low and uniform, with the exception of MSH, which was a comparatively better determinant of diversity than other structural components for Simpson (diversity), Berger-Parker and Taxon Richness (Fig. 6.3a). The averaged full-model Akaike weightings also showed MSH as overall the leading determinant of invertebrate diversity at ground level (Table 6.12). Accordingly, Kruskal-Wallis tests showed a significant difference between the averaged weightings of each explanatory variable, with MSH being the most prominent factor in *post hoc* tests (Table 6.13). Measures of invertebrate diversity in the hedge bottom all had a significant positive relationship with MSH, indicating increase in diversity with increase in sward height (Table 6.14).

At canopy level, GL (indicator of vegetation density) was the most conspicuous factor explaining Taxon Richness (TR), whereas Margin Width (MW) alone appeared to be the key factor for Simpson (diversity), but no other measure (Table 6.11b & Fig. 6.3b). The w_i values indicated that the probability of top models being the best explanatory factors for diversity in the hedge top was at most 30% and for the most part lower. In fact, in common with the results of modelling of invertebrate diversity at hedge bottom, Akaike values for variables explaining diversity of hedge canopy invertebrates were on the whole rather low and also showed a degree of uniformity (Table 6.12 & Fig. 6.3b). Overall there was no significant difference between the explanatory values of any of the model components describing ground vegetation structure (Table 6.13), and data were not further explored with correlations.

Table 6.7. Best models ($\Delta i \leq 2$) predicting abundance of invertebrate taxa in hedgerows at ground level (upper table) and canopy level (lower table), using measures of vegetation structure as explanatory variables. Total abundance (all taxa) only shown. Variables: CQ = ground cover as measured within 2 x 1m quadrats; GL = light conditions, measured in Lux, at ground level; MSH = maximum sward height; MW = margin width

Ground level						
Candidate models	**k**	**AICc**	**Δi**	**w_i**	**acc w_i**	**ER**
Total (all taxa)						
MSH + GL	3	593.56	0.00	0.25	0.25	---
GL	2	594.43	0.87	0.16	0.41	1.54
CQ + MSH + GL	4	595.24	1.68	0.11	0.51	2.32
CQ + MSH + MW	4	595.54	1.98	0.09	0.60	2.69
MSH + GL + MW	4	595.54	1.98	0.09	0.70	2.69
Canopy level						
Candidate models	**k**	**AICc**	**Δi**	**wi**	**acc wi**	**ER**
Total (all taxa)						
GL	2	452.05	0.00	0.36	0.36	---
MSH + GL	3	453.20	1.15	0.20	0.56	1.78

Table 6.8. Comparison of the averaged Akaike weightings for each measure of ground-level vegetation structure used as explanatory variables for invertebrate abundance at both hedge bottom (upper table) and hedge canopy (lower table). Values for mean, median, ±SD and ±SE are shown

Analysis - explanatory variables		**Akaike Mean (n=11)**	**Akaike Median (n=11)**	**±SD**	**±SE**
Ground level	**Invertebrate abundance**				
(Sticky traps)	Ground Cover	0.595	0.542	0.236	0.074
	Maximum Sward Height	0.765	0.819	0.249	0.079
	Ground Light	0.518	0.360	0.293	0.093
	Margin Width	0.418	0.392	0.149	0.047
Canopy level	**Invertebrate abundance**				
(Beating)	Ground Cover	0.397	0.317	0.167	0.053
	Maximum Sward Height	0.513	0.379	0.308	0.097
	Ground Light	0.798	0.850	0.234	0.074
	Margin Width	0.345	0.304	0.101	0.032

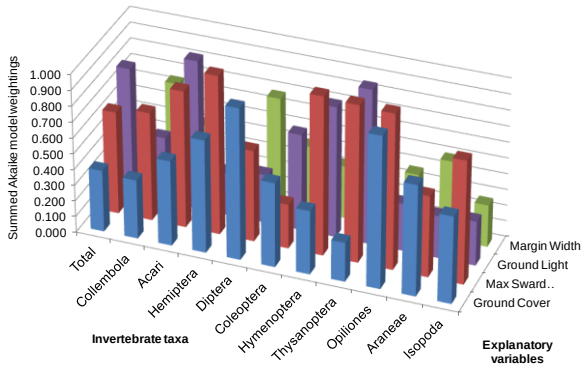
Table 6.9. Results of Kruskal-Wallis tests (*H*) on differences between the Akaike weightings of the measures of ground-level vegetation structure as candidate variables explaining abundance of hedgerow invertebrates in the hedge bottom (upper table) and hedge canopy (lower table). Post hoc Mann-Whitney *U* tests show comparisons between paired variables. Significant results are in bold. Asterisk indicates the more highly weighted variable

		Kruskal-Wallis				Post hoc tests		
Analysis - dependent variables		**n**	**df**	***H***	***p***	***U***	***p***	
Sticky traps (Ground level)	**Taxonomic Abundance**	11	3	9.90	0.190		ns	
Beatings (Canopy level)	**Taxonomic Abundance**	11	3	**17.07**	**0.001**	**6.00**	**<0.001**	**GL* v MW**
						8.00	**0.001**	**CQ v GL***
						24.50	**0.018**	**GL* v MSH**

Table 6.10. Spearman rank correlations between invertebrate abundance at canopy level (all invertebrates summed and top 10 most abundant taxa) and GL (ground level light). Significant relationships are highlighted in bold and shaded. An FDR-corrected significance level of 0.017 was applied

Taxa	**n**	r_s	***p***
Total Abundance (all taxa)	83	**-0.496**	**<0.001**
Collembola	83	**-0.491**	**<0.001**
Hemiptera	83	**-0.421**	**<0.001**
Acari	83	**-0.399**	**<0.001**
Araneae	83	-0.161	0.145
Coleoptera	83	**-0.301**	**0.006**
Hymenoptera	83	**-0.342**	**0.002**
Thysanoptera	83	**-0.277**	**0.011**
Psocoptera	83	-0.199	0.071
Diptera	83	**-0.287**	**0.009**
Lepidoptera	83	-0.176	0.111

(a)



(b)

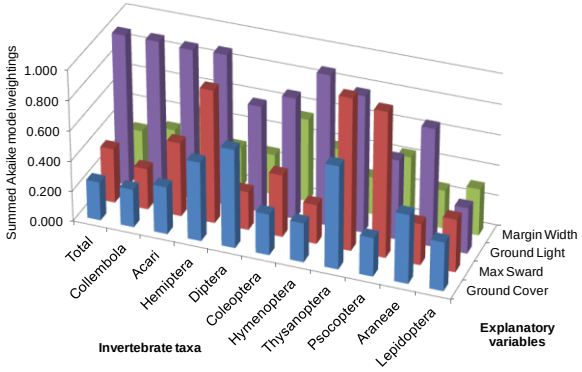
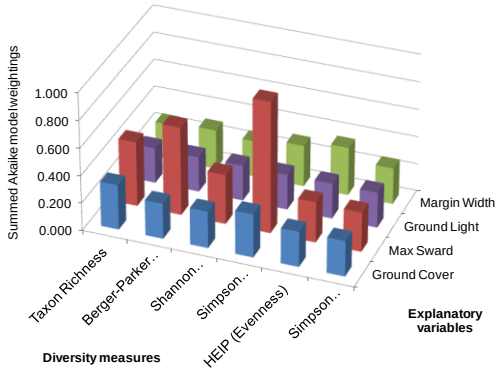


Figure 6.2a-b. Summed Akaike model weights for structural measures of ground vegetation potentially explaining invertebrate abundance at: (a) ground level, and (b) canopy level. Top 10 most abundant taxa only are shown for hedge bottom and hedge top respectively, as well as Total abundance (all taxa). Explanatory variables: Ground Cover; Ground Light; Max sward (height); Margin Width

(a)



(b)

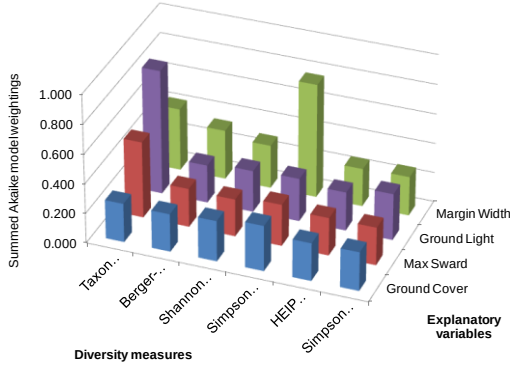


Figure 6.3a-b. Summed Akaike model weights for structural elements of ground vegetation potentially explaining measures of invertebrate diversity (Taxon Richness, Berger-Parker, Shannon, Simpson, Heip, Simpson Evenness) at: (a) ground level, and (b) canopy level. Explanatory variables: Ground Cover; Ground Light; Max Sward (height); Margin Width

Table 6.11a. Best candidate models ($\Delta i \leq 2$) predicting diversity of invertebrate taxa in hedgerows at ground level using measures of vegetation structure as potential explanatory variables. Variables: CQ = ground cover as measured within 2 x 1m quadrats; GL = light conditions, measured in Lux, at ground level; MSH = maximum sward height; MW = margin width

Candidate models	k	AICc	Δi	w_i	acc w_i	ER
Taxon Richness						
Intercept only	1	23.01	0.00	0.20	0.20	---
MSH	2	23.30	0.29	0.17	0.37	1.15
CQ	2	24.50	1.49	0.09	0.46	2.10
CQ + MSH	3	24.61	1.60	0.09	0.55	2.23
Berger-Parker						
MSH	2	41.07	0.00	0.25	0.25	---
Intercept only	1	42.25	1.18	0.14	0.39	1.81
MSH + MW	3	42.87	1.80	0.10	0.49	2.46
Shannon						
Intercept only	1	15.01	0.00	0.25	0.25	---
MSH	2	16.14	1.13	0.14	0.40	1.76
CQ	2	17.01	2.00	0.09	0.49	2.71
Simpson (Diversity)						
MSH	2	71.68	0.00	0.33	0.33	---
CQ + MSH	3	73.12	1.44	0.16	0.49	2.06
MSH + MW	3	73.28	1.60	0.15	0.64	2.23
HEIP (Evenness)						
Intercept only	1	12.23	0.00	0.28	0.28	---
MSH	2	13.95	1.72	0.12	0.41	2.36
Simpson (Evenness)						
Intercept only	1	11.53	0.00	0.29	0.29	---
MSH	2	13.33	1.80	0.12	0.40	2.46

Table 6.11b. Best candidate models ($\Delta i \leq 2$) predicting diversity of invertebrate taxa in hedgerows at canopy level using measures of vegetation structure as potential explanatory variables. Variables: CQ = ground cover as measured within 2 x 1m quadrats; GL = light conditions, measured in Lux, at ground level; MSH = maximum sward height; MW = margin width

Candidate models	k	AICc	Δi	w_i	acc w_i	ER
Taxon Richness						
GL	2	53.24	0.00	0.18	0.18	---
MSH + GL	3	53.24	0.00	0.18	0.36	1.00
GL + MW	3	53.79	0.55	0.14	0.49	1.32
MSH + GL + MW	4	53.84	0.60	0.13	0.63	1.35
Berger-Parker						
Intercept only	1	37.32	0.00	0.27	0.27	---
MW	2	38.67	1.35	0.14	0.41	1.96
Shannon						
Intercept only	1	10.92	0.00	0.28	0.28	---
MW	2	12.83	1.91	0.11	0.39	2.60
Simpson (Diversity)						
MW	2	77.91	0.00	0.27	0.27	---
CQ + MW	3	79.50	1.59	0.12	0.40	2.22
MSM + MW	3	79.78	1.87	0.11	0.50	2.55
GL + MW	3	79.84	1.93	0.10	0.61	2.63
HEIP (Evenness)						
Intercept only	1	11.71	0.00	0.30	0.30	---
Simpson (Evenness)						
Intercept only	1	18.82	0.00	0.28	0.28	---
GL	2	20.37	1.55	0.13	0.40	2.17
MW	2	20.82	2.00	0.10	0.50	2.72

Table 6.12. Comparison of the averaged Akaike weightings for each measure of ground-level vegetation structure used as explanatory variables for invertebrate diversity at both hedge bottom (upper table) and hedge canopy (lower table). Values for mean, median, ±SD and ±SE are shown

Analysis of explanatory variables		Akaike Mean n = 6	Akaike Median n = 6	±SD	±SE
Ground level (Sticky traps)	**Invertebrate diversity**				
	Ground Cover	0.280	0.263	0.032	0.013
	Maximum Sward Height	0.500	0.415	0.258	0.105
	Ground Light	0.257	0.257	0.001	0.000
	Margin Width	0.287	0.275	0.034	0.014
Canopy level (Beating)	**Invertebrate diversity**				
	Ground Cover	0.269	0.261	0.020	0.008
	Maximum Sward Height	0.303	0.258	0.104	0.042
	Ground Light	0.373	0.285	0.228	0.093
	Margin Width	0.389	0.312	0.195	0.080

Table 6.13. Results of Kruskal-Wallis tests (*H*) on differences between the Akaike weightings of the measures of ground-level vegetation structure as candidate variables explaining diversity of hedgerow invertebrates in the hedge bottom (upper table) and hedge canopy (lower table). Post hoc Mann-Whitney *U* tests show comparisons between paired variables. Significant results are highlighted in bold. Asterisk indicates the more highly weighted variable

Analysis - dependent variables		Kruskal-Wallis n	df	*H*	*p*	Post hoc tests *U*	*p*	
Sticky traps (Ground level)	**Diversity**	6	3	**15.20**	**0.002**	**0.00**	**0.004**	**GL v MSH***
						4.00	**0.025**	**CQ v MSH***
						5.00	**0.037**	**MSH* v MW**
						0.00	**0.004**	**GL v MW***
						5.50	**0.038**	**CQ* v GL**
Beatings (Canopy level)	**Diversity**	6	3	4.95	0.175		ns	

Table 6.14. Spearman rank correlations between invertebrate diversity at ground level and MSH (maximum sward height). All months combined. Significant relationships are highlighted. An FDR-corrected significance level of 0.02 was applied

Measures of diversity	n	r_s	*p*
Taxon Richness	**95**	**0.357**	**<0.001**
Berger-Parker	**95**	**0.311**	**0.002**
Shannon	**95**	**0.382**	**<0.001**
Simpson (Diversity)	**95**	**0.347**	**0.001**
Heip (Evenness)	**95**	**0.291**	**0.004**
Simpson (Evenness)	**95**	**0.290**	**0.004**

6.3.3. Hedge Structure – effects on invertebrate abundance and diversity

Canopy light (CL) penetration averaged 15.78% (±SD 15.88) overall for all months (April, July, September) combined. There was no significant difference between Mature (n = 48) and New (n = 47) hedges (Mann-Whitney U = 1047.50, n_1 = 48, n_2 = 47, p = 0.549).

Height (HA) averaged 2.96m (±SD 0.89) for all hedges combined (n = 32). Mature hedges (n = 16) were on average taller than New hedges (n = 16): 3.50m (±SD 0.84) versus 2.41m (±SD 0.54). This difference was significant (Mann-Whitney U = 31.50, n_1 = 16, n_2 = 16, p = <0.001).

Height Growth (HG) for all hedges (n = 32) averaged 32cm (±SD 33) over the period March to August 2011. There was no significant difference between the growth of Mature versus New hedges (Mann-Whitney U = 94.00, n_1 = 16, n_2 = 16, p = 0.199).

Canopy overhang/width (COA) for all hedges (n = 32) averaged 1.47m (±SD 0.69). Mature hedge canopies (n = 16) were on average wider than New hedges (n = 16): 1.81m (±SD 0.76) versus 1.12m (±SD 0.40). This difference was significant (Mann-Whitney U = 54.00, n_1 = 16, n_2 = 16, p = 0.005).

The mean canopy width growth (WG) over the period March to August for all hedges combined (n = 32) was 27cm (±SD 28). There was no significant difference between the growth of Mature versus New hedges (Mann-Whitney U = 85.00, n_1 = 16, n_2 = 16, p = 0.105).

The mean height of the canopy above ground (HAA) was 50cm (±SD 17) for all hedges combined (n = 32). Mature hedge canopies (n = 16) were on average higher above the ground than New hedge canopies (n = 16): 56.50cm (±SD 11.80) versus 42.50cm (±SD 18.40). The difference between the two hedge types was significant (Mann-Whitney U = 69.50, n_1 = 16, n_2 = 16, p = 0.027).

6.3.3.i. Invertebrate abundance

Hedgerow/canopy height (HG = Height Growth & HAA = Height Above Ground), but not measures of width, were the most important of the variables explaining total abundance at ground level, contributing to all top models (Table 6.15). By contrast, CL (Canopy Light – a measure of foliage/woody density) appeared prominently in the top models for the majority of individual taxa, excepting Diptera, Coleoptera and Araneae, for which width (COA) and height of canopy (HA) and height above ground (HAA) were more important (Appendix D, Table D7). Summed full model weightings showed CL as the main explanatory variable (Fig. 6.4a). CL was also the most highly weighted of model

components explaining invertebrate abundance in general, whereby the Akaike values implied a 70% probability that CL would be a component of the explanatory models (Table 6.16). Kruskal-Wallis tests showed a significant difference between the averaged weightings of the variables, with CL relatively important compared with the rest (Table 6.17). The relationship between CL and invertebrate abundance at ground level was significant for only Hymenoptera (r_s = -0.351, p = <0.001) and Thysanoptera (r_s = -0.369, p = <0.001). This was a weak/approaching moderate negative relationship with CL at ground level, indicating that as light levels decreased (density of vegetation increased), then the abundance of these organisms increased (see also Appendix D, Table D8). Measures of HG (growth in height) and height above ground (HAA - gap between the ground and the beginning of the canopy) were also identified in the *post hoc* tests (Table 6.17), but showed no correlation with either total invertebrate abundance or with numbers of individual taxa when tested by Spearman's correlations (Appendix D, Tables D9 & D10).

Canopy light (CL) was also the key factor in explaining total invertebrate abundance at canopy level (Table 6.15). In fact, CL alone was the top 'model' for explaining total abundance and contributed to top models for all individual taxa (Table 6.15; Appendix D, Table D11). Summed full model weightings showed that CL was a more important factor for some taxa than others, *e.g*. Hemiptera, Hymenoptera and Psocoptera (Fig. 6.4b). In fact, correlations showed that Psocoptera had the strongest relationship of any taxa with CL (and by extension vegetation density) (Table 6.18). For some taxa such as Araneae which had showed a significant relationship with CL at ground level, there was no significant correlation with CL in the canopy. In the case of Coleoptera and Diptera only there was no significant association with this measure of density at either ground- or canopy-level. Overall, averaged Akaike weightings showed that CL was, by a clear margin, the top variable explaining invertebrate abundance generally at canopy level, as it had been at ground level (Table 6.16): values indicated a relatively high probability (63%) that this variable belonged to the best models explaining invertebrate abundance in the hedge top. Kruskal-Wallis and post hoc tests showed a significant difference between weightings of all explanatory factors relating to hedge structure, whereby CL was the most prominent, although measures of both height and width also appeared to be comparatively important (Table 6.17). Spearman rank correlations showed a significant relationship between invertebrate abundance in the hedge canopies and CL (Table 6.18), as had been shown for invertebrates in the hedge base. CL was significantly negatively associated with

the total number of invertebrates at canopy level. There was also a significant negative relationship between CL and half of the individual taxa (Table 6.18). Height and width were also identified in the post hoc tests as being of interest as a factor in canopy invertebrate abundance. Height (HA) was in fact significantly correlated with abundance of only two taxa in the hedge top: Hemiptera (r_s = 0.345, p = 0.001) and Lepidoptera (r_s = 0.283, p = 0.009). Width (COA) showed a significant relationship with numbers of Lepidoptera only ((r_s = 0.295, p = 0.007). In addition, the measure of hedge height growth (HG) was significantly correlated with Araneae (r_s = 0.442, p = <0.001). The full correlations are shown in Appendix D, Tables D12-D14.

6.3.3.ii. Invertebrate diversity

Canopy Light (CL), and therefore density of vegetation, featured amongst the top models explaining all measures of diversity at ground level (Table 6.19a). This was also possibly interlinked with height of canopy above ground (HAA), which also made a clear contribution, but other measures of dimensions less so. Intercept was however ranked above even the best models for 4 out of the 6 diversity measures, indicating that the selected variables possibly represented relatively weak explanatory factors. In the full model analysis, CL was the most conspicuous hedge structure model component explaining diversity at ground level, notably for Simpson diversity (Fig. 6.5a), and had a significantly higher weighting than other factors describing hedge structure (Tables 6.20 & 6.21). There was a significant, albeit weak, negative relationship between CL and all measures of invertebrate diversity in the hedge bottom, except Taxon Richness for which the relationship was also negative but non-significant (Table 6.22). The negative relationship indicates that as CL increased, *i.e.* canopy vegetation became thinner and a higher % of light penetrated the canopy, so ground-level diversity decreased. Although HAA seemed to be of interest in the full model analysis, there were no correlations between it and any diversity measure (Appendix D, Table D15).

The top models for hedge structure showed that CL was also relatively important factor in explaining invertebrate Taxon Richness at canopy level (Fig. 6.5b; Table 6.19b), and was a component of top models for Berger-Parker and Simpson, but in combination with aspects of height. For Shannon and evenness measures, however, CL proved no better than intercept. In the averaged full model for all diversity measures, CL was the most highly weighted structural variable (Table 6.20). Kruskal-Wallis tests however showed no significant difference between its effect on any diversity measure and that of other hedge structure variables at canopy level (Table 6.21).

Table 6.15. Best models ($\Delta i \leq 2$) explaining the abundance of invertebrate taxa in hedgerows at ground level (upper table) and canopy level (lower table), using measures of hedge structure as explanatory variables. Explanatory variables: CL = Canopy light penetration; COA = Canopy width; HA = Height; HAA = Height of canopy above ground; HG = Height growth

Ground level						
Candidate models	**k**	**AICc**	**Δi**	**w_i**	**acc w_i**	**ER**
Total (all taxa)						
HG + HAA	3	596.66	0	0.13	0.13	---
HG + HAA + CL	4	597.24	0.58	0.10	0.23	1.34
HA + HG + HAA	4	598.34	1.68	0.06	0.29	2.32
HG + COA + HAA	4	598.34	1.68	0.06	0.34	2.32
Canopy Level						
Candidate models	**k**	**AICc**	**Δi**	**w_i**	**acc w_i**	**ER**
Total (all taxa)						
CL	2	456.55	0	0.12	0.12	---
HG + CL	3	457.20	0.65	0.09	0.21	1.39
HG + COA + CL	4	457.51	0.96	0.08	0.29	1.62
HA + HG + CL	4	457.61	1.06	0.07	0.36	1.7
HA + CL	3	458.00	1.45	0.06	0.42	2.07
COA + CL	3	458.1	1.55	0.06	0.48	2.17

Table 6.16. Comparison of the averaged full model Akaike weightings for each measure of hedge structure used as explanatory variables for invertebrate abundance (total abundance and top 10 most abundant taxa) at both hedge bottom (upper table) and hedge canopy (lower table). Values for mean, median, ±SD and ±SE are shown

Analysis - explanatory variables		**Akaike Mean n = 11**	**Akaike Median n = 11**	**±SD**	**±SE**
Ground level (Sticky traps)	**Invertebrate abundance**				
	Height	0.480	0.412	0.231	0.073
	Height Growth	0.461	0.400	0.146	0.046
	Width	0.398	0.329	0.145	0.046
	Width Growth	0.307	0.294	0.058	0.018
	Height Above Ground	0.535	0.408	0.260	0.082
	Canopy Light	0.700	0.799	0.303	0.096
Canopy level (Beating)	**Invertebrate abundance**				
	Height	0.499	0.457	0.160	0.051
	Height Growth	0.496	0.394	0.236	0.074
	Width	0.421	0.357	0.120	0.038
	Width Growth	0.311	0.273	0.089	0.028
	Height Above Ground	0.467	0.394	0.248	0.078
	Canopy Light	0.630	0.585	0.282	0.089

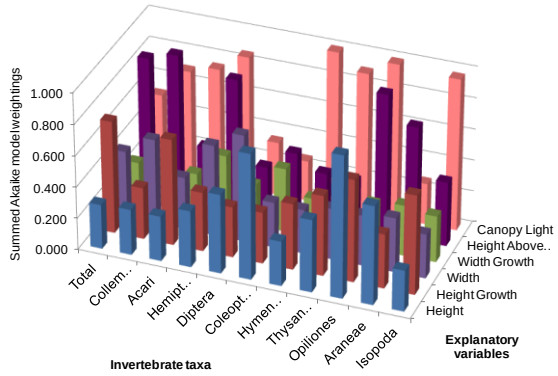
Table 6.17. Results of Kruskal-Wallis tests (*H*) on differences between the Akaike weightings of the measures of hedge structure as candidate variables explaining abundance of hedgerow invertebrates (total abundance and top 10 most abundant taxa) in the hedge bottom (upper table) and hedge canopy (lower table). Significant results are highlighted in bold. Mann-Whitney *U* post hoc tests indicate differences between paired variables. Asterisk marks the more highly weighted variables

		Kruskal-Wallis				Post hoc tests		
Analysis - dependent variables		**n**	**df**	***H***	***p***	***U***	***p***	
Sticky traps	**Taxonomic Abundance**	11	5	**13.92**	**0.016**	**21.00**	**0.009**	**CL* v WG**
(Ground level)						**30.00**	**0.045**	**CL* v W**
						16.00	**0.003**	**HG* v WG**
						22.50	**0.013**	**HAA* v WG**
Beatings	**Taxonomic Abundance**	11	5	**17.77**	**0.003**	**12.00**	**0.001**	**HA* v WG**
(Canopy level)						**11.00**	**0.001**	**CL* v WG**
						30.00	**0.045**	**CL* v HAA**
						22.00	**0.011**	**HG* v WG**
						16.00	**0.003**	**COA* v WG**

Table 6.18. Spearman rank correlations between invertebrate abundance (all taxa summed and top ten individual taxa) at canopy level and CL (canopy light levels). All months combined. Significant results highlighted in bold and shaded. An FDR-corrected significance level of 0.017 has been applied

Taxa	**n**	r_s	***p***
Total Abundance (all taxa)	**83**	**-0.459**	**<0.001**
Collembola	**83**	**-0.382**	**<0.001**
Hemiptera	**83**	**-0.423**	**<0.001**
Acari	83	-0.192	0.082
Araneae	**83**	**-0.389**	**<0.001**
Coleoptera	83	-0.190	0.085
Hymenoptera	**83**	**-0.414**	**<0.001**
Thysanoptera	83	-0.226	0.040
Psocoptera	**83**	**-0.460**	**<0.001**
Diptera	83	-0.106	0.342
Lepidoptera	83	-0.164	0.138

(a)



(b)

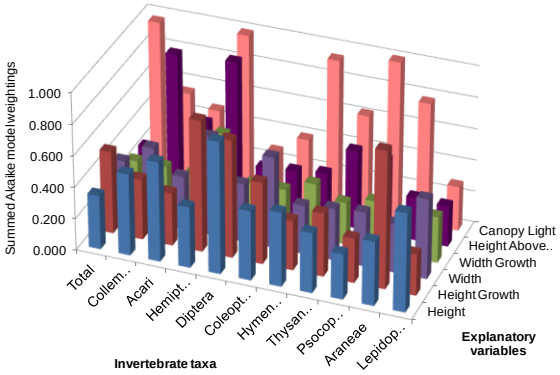
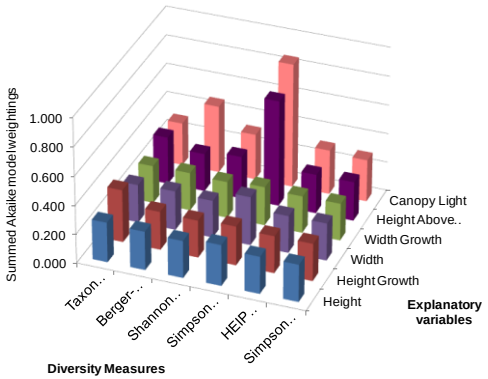


Figure 6.4a-b. Summed Akaike full model weights for measures of hedge structure potentially explaining invertebrate abundance at: (a) ground level, and (b) canopy level. Top ten most abundant taxa at hedge bottom and hedge canopy are shown, as well as Total abundance (all taxa). Variables: Canopy Light; Height Above Ground; Width Growth; Width; Height Growth; Height

(a)



(b)

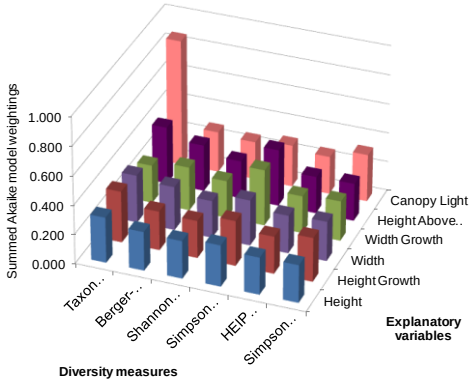


Figure 6.5a-b. Summed Akaike full model weights for aspects of hedge structure potentially explaining measures of invertebrate diversity (Taxon Richness, Berger-Parker, Shannon, Simpson, Heip, Simpson Evenness) at: (a) ground level, and (b) canopy level. Variables: Canopy Light; Height Above Ground; Width Growth; Width; Height Growth; Height

Table 6.19a. Best models ($\Delta i \leq 2$) explaining invertebrate diversity in hedgerows at ground level using measures of hedge structure as explanatory variables: CL = Canopy light penetration; COA = Canopy width; HA = Height; HAA = Height of canopy above ground; HG = Height growth; WG = Width growth

Candidate models	k	AICc	Δi	w_i	acc w_i	ER
Taxon Richness						
Intercept	1	23.01	0	0.12	0.12	---
HG	2	24.09	1.08	0.07	0.19	1.71
HAA	2	24.30	1.29	0.06	0.25	1.90
CL	2	24.93	1.92	0.05	0.30	2.61
Berger-Parker						
HAA + CL	3	41.91	0	0.08	0.08	---
CL	2	41.98	0.07	0.08	0.17	1.03
Intercept	1	42.25	0.34	0.07	0.24	1.18
HAA	2	42.90	0.99	0.05	0.29	1.64
Shannon						
Intercept	1	15.01	0	0.15	0.15	---
CL	2	16.59	1.58	0.07	0.21	2.20
HAA	2	16.75	1.74	0.06	0.27	2.38
Simpson (Diversity)						
HAA + CL	3	72.74	0	0.16	0.16	---
COA + HAA + CL	4	73.83	1.09	0.09	0.26	1.73
HA + HAA + CL	4	74.30	1.56	0.07	0.33	2.18
Heip (Evenness)						
Intercept	1	12.23	0	0.15	0.15	---
CL	2	13.85	1.62	0.07	0.22	2.25
HAA	2	14.20	1.97	0.06	0.28	2.67
Simpson (Evenness)						
Intercept	1	11.53	0	0.15	0.15	---
CL	2	13.31	1.78	0.06	0.22	2.43
HAA	2	13.49	1.96	0.06	0.28	2.66

Table 6.19b. Best models ($\Delta i \leq 2$) explaining invertebrate diversity in hedgerows at canopy level using measures of hedge structure as explanatory variables: CL = Canopy light penetration; COA = Canopy width; HA = Height; HAA = Height of canopy above ground; HG = Height growth; WG = Width growth

Candidate models	k	AICc	Δi	w_i	acc w_i	ER
Taxon Richness						
CL	2	52.10	0.00	0.13	0.13	---
HAA + CL	3	52.97	0.87	0.08	0.21	1.55
HA + CL	3	53.61	1.51	0.06	0.27	2.13
COA + CL	3	53.74	1.64	0.06	0.33	2.27
Berger-Parker						
Intercept	1	37.32	0.00	0.12	0.12	---
HAA	2	38.62	1.30	0.07	0.19	1.92
WG	2	38.67	1.35	0.06	0.25	1.96
COA	2	39.11	1.79	0.05	0.30	2.45
HG	2	39.25	1.93	0.05	0.35	2.63
CL	2	39.32	2.00	0.05	0.40	2.72
Shannon						
Intercept	1	10.92	0.00	0.16	0.16	---
Simpson (Diversity)						
Intercept	1	80.29	0.00	0.07	0.07	---
WG	2	80.33	0.04	0.07	0.15	1.02
HAA	2	80.41	0.12	0.07	0.22	1.06
HG	2	81.49	1.20	0.04	0.26	1.82
WG + HAA	3	81.67	1.38	0.04	0.30	2.00
CL	2	81.69	1.40	0.04	0.33	2.01
COA	2	81.99	1.70	0.03	0.36	2.34
COA + HAA	3	82.14	1.85	0.03	0.39	2.53
HAA + CL	3	82.18	1.89	0.03	0.42	2.58
HG + WG	3	82.19	1.90	0.03	0.45	2.59
WG + CL	3	82.26	1.97	0.03	0.48	2.68
Heip (Evenness)						
Intercept	1	11.71	0.00	0.16	0.16	---
Simpson (Evenness)						
Intercept	1	18.82	0.00	0.13	0.13	---
CL	2	20.04	1.22	0.07	0.20	1.84
HG	2	20.40	1.58	0.06	0.26	2.20
WG	2	20.53	1.71	0.06	0.31	2.35
COA	2	20.72	1.90	0.05	0.36	2.59
HAA	2	20.79	1.97	0.05	0.41	2.68

Table 6.20. Comparison of the averaged Akaike weightings for each measure of hedge structure used as explanatory variables for invertebrate diversity at both hedge bottom (upper table) and hedge canopy (lower table). Values for mean, median, ±SD and ±SE are shown

Analysis - explanatory variables		Akaike Mean n = 6	Akaike Median n = 6	±SD	±SE
Ground level	**Invertebrate diversity**				
(Sticky traps)	Height	0.266	0.262	0.011	0.005
	Height Growth	0.278	0.262	0.041	0.017
	Width	0.273	0.260	0.031	0.013
	WidthGrowth	0.259	0.258	0.006	0.002
	Height Above Ground	0.359	0.282	0.184	0.075
	Canopy Light	0.422	0.312	0.223	0.091
Canopy level	**Invertebrate diversity**				
(Beating)	Height	0.272	0.262	0.022	0.009
	Height Growth	0.290	0.284	0.038	0.015
	Width	0.287	0.285	0.029	0.012
	WidthGrowth	0.287	0.266	0.050	0.020
	Height Above Ground	0.311	0.288	0.065	0.027
	Canopy Light	0.378	0.282	0.238	0.097

Table 6.21. Results of Kruskal-Wallis tests (*H*) on differences between the Akaike weightings of the measures of hedge structure as candidate variables explaining diversity of hedgerow invertebrates in the hedge bottom (upper table) and hedge canopy (lower table). Significant results are highlighted in bold. Mann-Whitney *U* post hoc tests indicate differences between paired variables. Asterisk marks the more highly weighted variables

		Kruskal-Wallis				Post hoc tests		
Analysis - dependent variables		**n**	**df**	***H***	***p***	***U***	***p***	
Sticky traps	**Diversity**	6	5	**16.63**	**0.005**	**0.00**	**0.004**	**CL* v HA**
(Ground level)						**0.00**	**0.004**	**CL* v WG**
						4.00	**0.025**	**CL* v HG**
						4.00	**0.025**	**CL* v COA**
						1.50	**0.008**	**WG v HAA***
Beatings	**Diversity**	6	5	2.02	0.846		ns	
(Canopy level)								

Table 6.22. Spearman rank correlations between measures of invertebrate diversity at ground level and CL (canopy light conditions). An FDR-corrected significance level of 0.02 has been applied

Measures of diversity	**n**	r_s	***p***
Taxon Richness	95	-0.115	0.267
Berger-Parker	**95**	**-0.280**	**0.006**
Shannon	**95**	**-0.269**	**0.008**
Simpson (Diversity)	**95**	**-0.273**	**0.007**
Heip (Evenness)	**95**	**-0.289**	**0.004**
Simpson (Evenness)	**95**	**-0.264**	**0.010**

6.3.4. Landscape context – effects on invertebrate abundance and diversity

Distance from woodland (DW) averaged 644.06 m (± SD 657.03) for all hedges combined (n = 32). On average, New hedges tended to be more distant from wooded areas than Mature hedges: 724.06 m (±SD 738.97) versus 564.06 (±SD 576.55) but there was no significant difference between the two hedge types (Mann-Whitney U = 115.50, n_1 = 16, n_2 = 16, p = 0.637).

For all hedges combined (n = 32) connections averaged 2.06 (±SD 1.05). Both New hedges and Mature hedges also averaged 2.06 connections (±SD 0.85 versus ±SD 1.24). No significant difference between the hedge age groups was found (Mann-Whitney U = 122.50, n_1 = 16, n_2 = 16, p = 0.828).

6.3.4.i. Invertebrate abundance

No single good model consisting of the selected landscape components could explain total invertebrate abundance (Table 6.23). Distance from Woodland (DW) was the only variable to appear in top models for all ground-level taxa (Appendix D, Table D16).

Location (L) was the most important factor for determining the abundance of 4 out of 10 individual taxa and in combination with Distance from Woodland (DW) for 3 others. Intercept ranked above variables in the top models for Araneae and Hymenoptera, suggesting that the selected landscape variables were not key explanatory factors in those cases (Appendix D, Table D16). Full model weightings showed that L was in fact the most prominent landscape factor overall in explaining ground-level abundance in the hedge bottom (Fig. 6.6a and Table 6.24). Kruskal-Wallis tests showed a significant difference between averaged weightings (all taxa) for the landscape model components, with *post hoc* tests identifying not only L but also DW as significant explanatory variables (Table 6.25). Swallow was identified as the key location for a number of taxa, but Potterhanworth, Riseholme and Nettleham were also important for one or two taxa (Table 6.26). Conversely, there were also 4 taxa for which Location appeared to make no difference (Table 6.26). After FDR correction for multiple testing, Spearman's correlations showed that no single taxon was significantly correlated with DW, despite its prominence in the top explanatory models (Appendix D, Table D17). Neither total abundance nor the abundance of any individual taxon at ground level had a strong relationship with DW. Certain correlations were negative, indicating a decrease in number as distance from woodland increased, but this was not at a significant level.

Distance from Woodland (DW) was the top landscape factor for explaining total abundance of all taxa at canopy level (Table 6.23) and featured in top models for all

individual taxa barring Acari (Appendix D, Table D18). Connectivity and Location also made contributions to models explaining invertebrate abundance at canopy level (Figure 6.6b), although even the best landscape models were ranked below intercept for 4 of the 10 most abundant taxa. Based on averaged full model Akaike weightings, DW was by a slim margin the top model component explaining invertebrate abundance in the hedge canopy (Table 6.24), but there was no statistically significant difference between the weightings of the variables and therefore no outstanding explanatory factor amongst them relating to the abundance of canopy-active invertebrates (Table 6.25).

6.3.4.ii. Invertebrate diversity

In explaining invertebrate diversity at ground level, Location (L) was less prominent than Connectivity (C) and Distance from Woodland (DW) (Fig. 6.7a & Table 6.27a). Only Connectivity featured among the top models for explaining ground-occurring invertebrate diversity (Table 6.27a). The intercept-only model was always ranked above top models, suggesting poor model fits for the selected landscape variables overall in relation to invertebrate diversity in the hedge bottom. Connectivity had a higher weighting than either DW or L, and Kruskal-Wallis tests showed that there was a significant difference between the full model weightings of these variables, with both C and DW making similar, albeit moderate, contributions to models compared with L (Tables 6.28 & 6.29). Neither C nor DW were however significantly correlated with any measure of invertebrate diversity when analysed by Spearman's ranked correlations (Appendix D, Tables D19 & D20).

Distance from Woodland (DW) featured in top models explaining invertebrate diversity at canopy level, but was no better than intercept (Table 6.27b). Summed full model weightings showed that Location (L) was generally a rather weaker factor than either Connectivity (C) or Distance from Woodland (DW) in accounting for canopy-active invertebrate diversity, with the exception of Taxon Richness (Fig. 6.7b). Full model averages for all diversity indices showed that DW had a higher weighting than either C or L, but no statistically significant difference between the component weightings was found (Tables 6.28 & 6.29), suggesting all landscape factors were equivalent - equally good or bad - at determining invertebrate diversity in the hedge top.

Table 6.23. Best models ($\Delta i \leq 2$) explaining the abundance of invertebrate taxa in hedgerows at ground level (upper table) and canopy level (lower table) using measures of landscape context as explanatory variables. Total invertebrate abundance only shown. Explanatory variables: C = connectivity (number of connections with other hedgerows); DW = distance from woodland; L = location

Ground level						
Candidate models	**k**	**AICc**	**Δi**	**w_i**	**acc w_i**	**ER**
Total (all taxa)						
Intercept	1	600.04	0	0.32	0.32	---
L	2	601.43	1.39	0.16	0.47	2
DW	2	601.73	1.69	0.14	0.61	2.32
DW & C	3	601.86	1.82	0.13	0.74	2.49
C	2	602.03	1.99	0.12	0.86	2.7
Canopy Level						
Candidate models	**k**	**AICc**	**Δi**	**w_i**	**acc w_i**	**ER**
Total (all taxa)						
DW	2	465.35	0	0.40	0.40	---
Intercept	1	466.95	1.6	0.18	0.58	2.22

Table 6.24. Comparison of the averaged Akaike weightings for measures of landscape context as explanatory variables for invertebrate abundance at both hedge bottom (upper table) and hedge canopy (lower table). Values for mean, median, ±SD and ±SE are shown

Analysis - explanatory variables		**Akaike Mean n = 11**	**Akaike Median n = 11**	**±SD**	**±SE**
Ground level	**Invertebrate abundance**				
(Sticky traps)	Distance from Woodland	0.421	0.373	0.136	0.043
	Location	0.601	0.613	0.285	0.090
	Connectivity	0.311	0.295	0.059	0.019
Canopy level	**Invertebrate abundance**				
(Beating)	Distance from Woodland	0.393	0.384	0.095	0.030
	Location	0.383	0.288	0.269	0.085
	Connectivity	0.311	0.297	0.060	0.019

Table 6.25. Results of Kruskal-Wallis tests (*H*) on differences between the Akaike weightings of the measures of landscape context as candidate variables explaining abundance of hedgerow invertebrates in the hedge bottom (upper table) and hedge canopy (lower table). Mann-Whitney *U* post hoc tests show significant differences only. Significant results are highlighted in bold. Asterisk indicates higher ranked variable

		Kruskal-Wallis				**Post hoc tests**		
Analysis - dependent variables		**n**	**df**	***H***	***p***	***U***	***p***	
Sticky traps (Ground level)	**Taxonomic Abundance**	11	2	**7.06**	**0.029**	**29.00** **26.00**	**0.039** **0.023**	**L* v C** **DW* v C**
Beatings (Canopy level)	**Taxonomic Abundance**	11	2	5.09	0.079		ns	

Table 6.26. Results of Kruskal-Wallis with post hoc Mann-Whitney tests showing the difference between the ground-level invertebrate abundance at the 4 different farm locations: Nettleham (N), Potterhanworth (P), Riseholme (R), Swallow (S). Significant results are highlighted in bold

	Kruskal-Wallis			Post hoc tests		
Taxa	**df**	***H***	***p***	***U***	***p***	
Total Abundance (all taxa)	3	6.287	0.098		ns	
Acari	3	**8.057**	**0.045**	**136.00**	**0.032**	**P v S***
				94.50	**0.014**	**R v S***
Coleoptera	3	**16.418**	**0.001**	**73.00**	**0.001**	**N v S***
				67.50	**<0.001**	**P v S***
				63.50	**0.001**	**R v S***
Collembola	3	**8.026**	**0.045**	**223.50**	**0.006**	**N v P***
Diptera	3	**17.803**	**<0.001**	**54.00**	**<0.001**	**N v S***
				64.50	**<0.001**	**P v S***
				87.00	**0.007**	**R v S***
Isopoda	3	**11.166**	**0.011**	**187.50**	**0.015**	**N v R***
				197.50	**0.004**	**P v R***
Opiliones	3	**8.891**	**0.031**	**245.50**	**0.017**	**N* v P**
				220.50	**0.015**	**P v R***
Araneae	3	2.926	0.403		ns	
Hemiptera	3	5.968	0.113		ns	
Hymenoptera	3	3.382	0.336		ns	
Thysanoptera	3	4.002	0.261		ns	

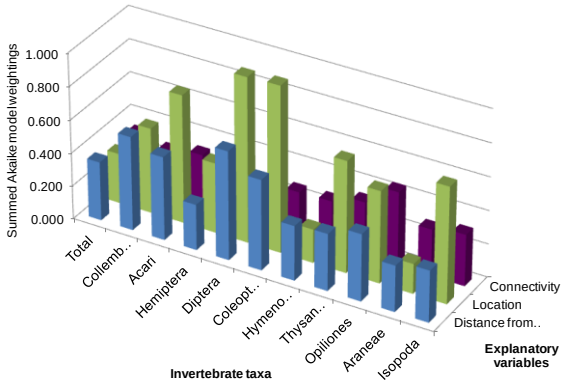
Table 6.27a. Best models ($\Delta i \leq 2$) explaining invertebrate diversity in hedgerows at ground level using measures of landscape context as explanatory variables. Key to variables: C = connectivity, *i.e.* number of connections with other hedgerows; DW = distance from woodland; L = location

Candidate models	k	AICc	Δi	w_i	acc w_i	ER
Taxon Richness						
Intercept	1	23.01	0.00	0.47	0.47	---
C	2	24.50	1.49	0.22	0.69	2.10
Berger-Parker						
Intercept	1	42.25	0.00	0.48	0.48	---
C	2	44.10	1.85	0.19	0.67	2.52
Shannon						
Intercept	1	15.01	0.00	0.52	0.52	---
Simpson (Diversity)						
Intercept	1	77.55	0.00	0.47	0.47	---
C	2	79.39	1.84	0.19	0.66	2.51
Heip (Evenness)						
Intercept	1	12.23	0.00	0.52	0.52	---
Simpson (Evenness)						
Intercept	1	11.53	0.00	0.52	0.52	---

Table 6.27b. Best models ($\Delta i \leq 2$) explaining invertebrate diversity in hedgerows at canopy level using measures of landscape context as explanatory variables. Key to variables: C = connectivity, *i.e.* number of connections with other hedgerows; DW = distance from woodland; L = location

Candidate models	k	AICc	Δi	w_i	acc w_i	ER
Taxon Richness						
L	2	56.25	0.00	0.28	0.28	---
Intercept	1	57.03	0.78	0.19	0.47	1.48
DW	2	57.27	1.02	0.17	0.63	1.67
Berger-Parker						
Intercept	1	37.32	0.00	0.48	0.48	---
C	2	39.19	1.87	0.19	0.67	2.55
DW	2	39.31	1.99	0.18	0.85	2.71
Shannon						
Intercept	1	10.92	0.00	0.53	0.53	---
DW	2	12.92	2.00	0.20	0.73	2.72
Simpson (Diversity)						
Intercept	1	80.29	0.00	0.41	0.41	---
Heip (Evenness)						
Intercept	1	11.71	0.00	0.52	0.52	---
Simpson (Evenness)						
Intercept	1	18.82	0.00	0.50	0.50	---
DW	2	20.69	1.87	0.20	0.70	2.55

(a)



(b)

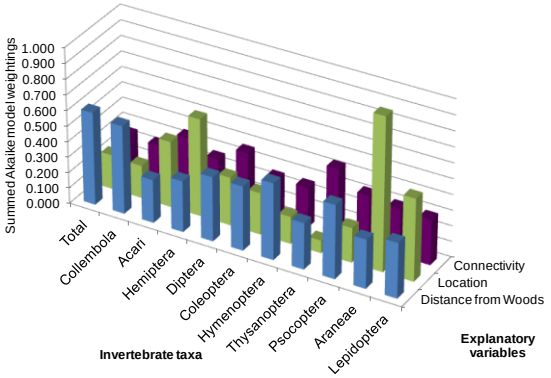
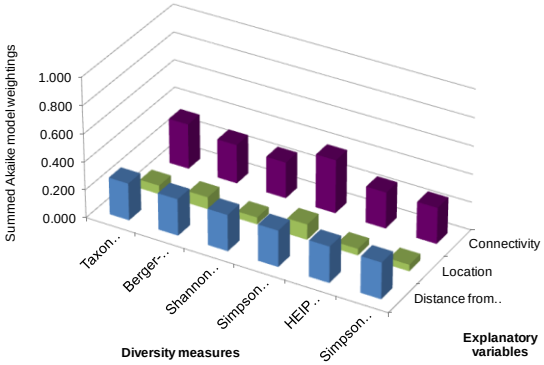


Figure 6.6a-b. Summed Akaike model weights for measures of landscape context potentially explaining invertebrate abundance at: (a) ground level, and (b) canopy level. Total abundance and top ten most abundant taxa at hedge bottom and hedge canopy are shown. Variables: Connectivity; Location; Distance from Woodland

(a)



(b)

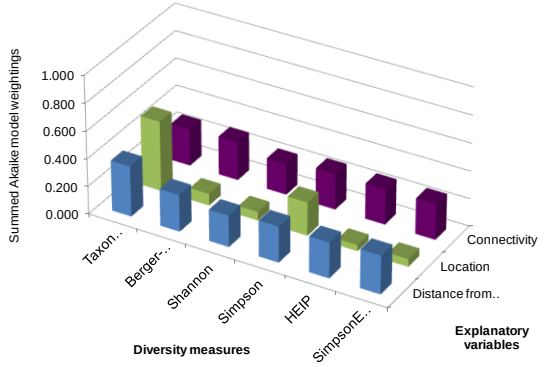


Figure 6.7a-b. Summed Akaike model weights for measures of landscape context potentially explaining measures of invertebrate diversity (Taxon Richness, Berger-Parker, Shannon, Simpson, Heip, Simpson Evenness) at: (a) ground level, and (b) canopy level. Variables: Connectivity; Location; Distance from Woodland

Table 6.28. Comparison of the averaged Akaike weightings for measures of landscape context as explanatory variables for invertebrate diversity at both hedge bottom (upper table) and hedge canopy (lower table). Values for mean, median, ±SD and ±SE are shown

Analysis - explanatory variables		Akaike Mean	Akaike Median	±SD	±SE
Ground level (Sticky traps)	**Invertebrate diversity**				
	Distance from Woodland	0.261	0.260	0.001	0.000
	Location	0.067	0.056	0.029	0.012
	Connectivity	0.294	0.269	0.054	0.022
Canopy level (Beating)	**Invertebrate diversity**				
	Distance from Woodland	0.277	0.264	0.047	0.019
	Location	0.166	0.074	0.182	0.074
	Connectivity	0.259	0.260	0.018	0.007

Table 6.29. Results of Kruskal-Wallis tests (*H*) on differences between the Akaike weightings of the measures of landscape context as candidate variables explaining diversity of hedgerow invertebrates in the hedge bottom (upper table) and hedge canopy (lower table). Mann-Whitney *U* post hoc tests show significant differences only. Significant results are highlighted in bold. Asterisk indicates more important variable

		Kruskal-Wallis				Post hoc tests		
Analysis - dependent variables		**n**	**df**	***H***	***p***	***U***	***p***	
Ground Level (Sticky traps)	**Diversity**	6	2	**11.38**	**0.003**	**0.00**	**0.004**	**C* v L**
						0.00	**0.004**	**DW* v L**
Canopy Level (Beating)	**Diversity**	6	2	4.40	0.111		ns	

6.3.5. Weather – effects on invertebrate abundance and diversity

Average Humidity per hedge trapping session for all months (April, July, September) combined (n = 95) was 71.46% (±SD 8.38), Rainfall averaged 0.82 mm (±SD 1.39), Temperature averaged 14.26^{0}C (±SD 2.77). Monthly averages were: in April, H = 72.17% (±SD 3.84), R = 0.33 mm (±SD 0.77), T = 11.47 (±SD1.66), W = 16.09 km/h (±SD 3.89); in July, H = 70.2% (±SD 12.37), R = 2.12 mm (±SD 1.60), T = 15.60^{0}C (±SD1.30), W = 15.67 km/h (±SD 3.03); in September, H = 72.03% (±SD 6.66), R = 0 mm, T = 15.75^{0}C (±SD 2.64), W = 15.94 km/h (±SD 1.47).

Rainfall was excluded from the models for canopy-level invertebrates since sampling via beating was never conducted during wet weather. Average Humidity per hedge trapping session for all months (April, July, September) combined (n = 83) was 40.86% (±SD 9.37), Temperature averaged 25.81^{0}C (±SD 5.14) and Wind speed 4.92 km/h (±SD 5.04). Monthly averages were: in April (n = 26), H = 41.32% (±SD 10.53), T = 22.82 (±SD 3.38), W = 6.09 km/h (±SD 5.04); in July (n = 31), H = 42.43 (±SD 9.59), T =

26.62^{0}C (±SD 5.27), W = 4.03 km/h (±SD 5.29; in September (n = 26), H = 38.53% (±SD 7.61), T = 27.82^{0}C (±SD 5.27), W = 4.80 km/h (±SD 4.68).

6.3.5.i. Invertebrate abundance

A combination of Temperature (T), Rainfall (R) and Wind speed (W) was the best model explaining total invertebrate abundance in the hedge bottom (Table 6.30). Both Temperature (T) and Rainfall (R) contributed to top models for all individual invertebrate taxa at ground level, whereas Wind Speed (W) and Humidity (H), while well-represented were not components of top models in all cases (Appendix D, Table D21). Humidity was the weakest of the explanatory factors overall, while Rainfall was the most heavily weighted variable determining invertebrate abundance at ground level (Fig. 6.8a). Rain was the most important model component explaining invertebrate abundance in general, followed by Temperature (Table 6.31). Kruskal-Wallis tests showed a significant difference between model weightings for each weather variable, with the principal differences lying between Rainfall and Humidity/Wind speed respectively (Table 6.32). Rainfall was significantly correlated with Total Abundance (all taxa) and significantly related with the majority of individual taxa (Table 6.33). Relationships were universally positive, indicating that as rain increased, so abundance of each taxon increased at hedge bottom. In addition, coefficients indicated a moderate to strong relationship with rainfall, the highest value coefficients of all explanatory variables modelled. Temperature was positively correlated with the abundance of the majority of taxa, and exhibited a significant relationship with numbers of 5 out of 10 individual taxa (Table 6.34). In the case of Collembola only, T was highly significantly *negatively* correlated with abundance.

Wind Speed (WSH) measured on the Silva handheld device was the most important factor in determining total invertebrate abundance in the hedge top, featuring in all top models (Table 6.30). It was also a prominent component of top models explaining the abundance of individual taxa at canopy level (Appendix D, Table D22). Its significance as a determinant of the abundance of canopy-active invertebrate taxa was indicated also by full model weightings (Table 6.31; Fig. 6.8b. Kruskal-Wallis tests indicated a significant difference between weather variable weightings, with Wind Speed being identified as a factor in post hoc testing (Table 6.32). The abundance of the majority of canopy-active invertebrates were significantly negatively correlated with WSH (Table 6.35), indicating a decrease in numbers sampled as wind speeds increased.

6.3.5.ii. Invertebrate diversity

Temperature (T) featured prominently in top models explaining invertebrate diversity at ground level (Table 6.36a). Its importance as a factor in diversity was evidenced also by the summed model weightings for weather variables (Fig. 6.9a). Temperature was the top weighted weather variable by a clear margin (Table 6.47). There was a significant difference between the weightings of weather conditions explaining overall diversity and *post hoc* tests identified Temperature as the most important model component, *i.e.* amongst weather variables the most important determinant of invertebrate diversity in the hedge bottom (Table 6.48). Temperature was significantly correlated with invertebrate diversity at hedge base, by all measures, indicating that as temperature increased, measures of invertebrate diversity increased in tandem (Table 6.49).

Wind Speed was identified as the key determinant of invertebrate abundance in the hedge canopy, but it was not markedly more important than other weather-related variables in explaining invertebrate diversity values (except for Taxon Richness) (Table 6.50 & Fig. 6.9b). On the whole Akaike values were low with a degree of uniformity. For most measures of diversity, the models ranked no better than the intercept-only model (Table). Averaged weightings of weather variables showed that Wind speed had the highest weighting (Table 6.47), Although no statistically significant difference was found between the 3 weather model components (Table 6.48). This suggested that all weather variables had more or less equivalent effect in determining the diversity of invertebrates present at canopy-level in the hedgerows.

Table 6.30. Best models ($\Delta i \leq 2$) explaining the total abundance of invertebrate taxa in hedgerows at ground level (upper table) and canopy level (lower table) using weather conditions as explanatory variables. Key to weather variables (ground level): H = humidity; R = rain; T = temperature; W = wind speed. Key to weather variables (canopy): HH = humidity handheld; TH = temperature handheld; WSH = wind speed handheld

Ground level						
Candidate models	**k**	**AICc**	**Δi**	**w_i**	**acc w_i**	**ER**
Total abundance (all taxa)						
T + W + R	4	565.84	0.00	0.44	0.44	---
W + R	3	566.76	0.92	0.28	0.72	1.58
Canopy level						
Candidate models	**k**	**AICc**	**Δi**	**w_i**	**acc w_i**	**ER**
Total abundance (all taxa)						
WSH	2	453.95	0.00	0.36	0.36	---
TH + WSH	3	454.00	0.05	0.35	0.71	1.03
TH + HH + WSH	4	455.61	1.66	0.16	0.86	2.30
HH + WSH	3	455.90	1.95	0.13	1.00	2.66

Table 6.31. Comparison of the averaged Akaike weightings for weather conditions used as explanatory variables for invertebrate abundance (total abundance and top 10 most abundant taxa) at both hedge bottom (upper table) and hedge canopy (lower table). Values for mean, median, ±SD and ±SE are shown

Analysis - explanatory variables		Akaike Mean (n = 11)	Akaike Median (n = 11)	±SD	±SE
Ground level	**Invertebrate abundance**				
(Sticky traps)	Rain	0.931	0.985	0.114	0.036
	Temperature	0.756	0.955	0.310	0.098
	Humidity	0.462	0.293	0.288	0.091
	Wind Speed	0.611	0.534	0.351	0.111
Canopy level	**Invertebrate abundance**				
(Beating)	Temperature	0.541	0.521	0.218	0.069
	Humidity	0.419	0.389	0.131	0.041
	Wind Speed	0.724	0.824	0.277	0.088

Table 6.32. Results of Kruskal-Wallis tests on differences between the Akaike weightings of weather conditions as candidate variables explaining abundance of hedgerow invertebrates in the hedge bottom (upper table) and hedge canopy (lower table). Significant results are highlighted in bold. Mann-Whitney pairwise post hoc tests are shown for significant results only. Asterisks mark the significantly higher weighted variables

		Kruskal-Wallis				Post hoc tests		
Analysis - dependent variables		n	df	*H*	*p*	*U*	*p*	
Sticky traps (Ground level)	**Taxonomic Abundance**	11	3	**14.86**	**0.002**	**8.00**	**0.001**	**H v R***
						25.00	**0.020**	**R* v W**
						23.00	**0.014**	**H v T***
Beatings (Canopy level)	**Taxonomic Abundance**	11	2	**9.26**	**0.010**	**15.00**	**0.003**	**HH v WSH***

Table 6.33. Spearman rank correlations showing the relationship between rainfall and invertebrate abundance in the hedge bottom (total abundance of all taxa and abundance of top 10 most abundant taxa). All months combined: April, July, September. An FDR-corrected significance level of 0.017 was applied

Taxa	n	r_s	*p*
Total Abundance	**95**	**0.503**	**<0.001**
Collembola	95	0.071	0.494
Acari	**95**	**0.612**	**<0.001**
Hemiptera	**95**	**0.384**	**<0.001**
Diptera	**95**	**0.202**	**0.049**
Coleoptera	**95**	**0.460**	**<0.001**
Hymenoptera	**95**	**0.430**	**<0.001**
Thysanoptera	**95**	**0.610**	**<0.001**
Opiliones	95	0.123	0.235
Araneae	**95**	**0.282**	**0.006**
Isopoda	**95**	**0.207**	**0.044**

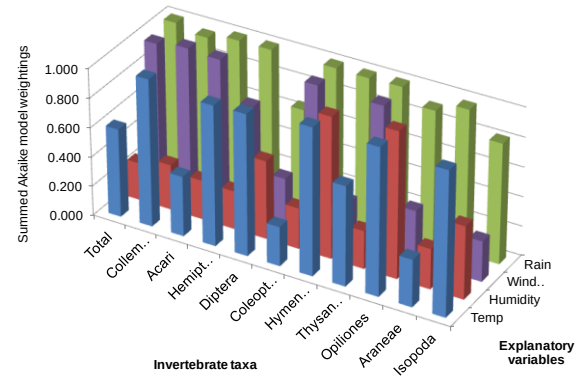
Table 6.34. Results of Spearman rank correlations showing the relationship between Temperature and invertebrate abundance in the hedge bottom (total abundance of all taxa and abundance of top 10 most abundant taxa). All months combined: April, July, September. An FDR-corrected significance level of 0.017 was applied

Taxa	n	r_s	*p*
Total Abundance	95	0.175	0.090
Collembola	**95**	**-0.248**	**0.015**
Acari	95	0.191	0.064
Hemiptera	**95**	**0.381**	**<0.001**
Diptera	**95**	**0.222**	**0.031**
Coleoptera	95	0.201	0.051
Hymenoptera	**95**	**0.470**	**<0.001**
Thysanoptera	95	0.190	0.065
Opiliones	**95**	**0.386**	**<0.001**
Araneae	95	0.166	0.108
Isopoda	**95**	**0.306**	**0.003**

Table 6.35. Results of Spearman rank correlations between Wind speed and canopy-active invertebrate abundance. All months combined: April, July, September. An FDR-corrected significance level of 0.017 was applied

Taxa	n	r_s	*p*
Total Abundance	**83**	**-0.483**	**<0.001**
Collembola	**83**	**-0.488**	**<0.001**
Hemiptera	83	-0.257	0.019
Acari	**83**	**-0.361**	**0.001**
Araneae	83	-0.145	0.191
Coleoptera	**83**	**-0.347**	**0.001**
Hymenoptera	83	-0.253	0.021
Thysanoptera	83	-0.168	0.129
Psocoptera	83	**-0.302**	**0.006**
Diptera	83	**-0.332**	**0.002**
Lepidoptera	83	-0.021	0.854

(a)



(b)

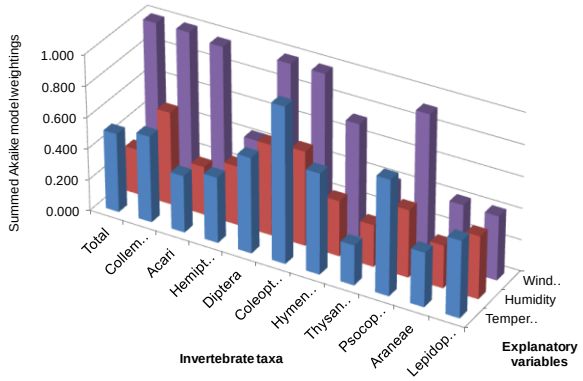
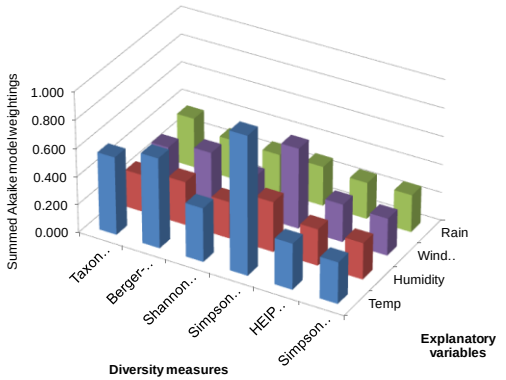


Figure 6.8a-b. Summed Akaike model weights for weather variables potentially explaining invertebrate abundance at: (a) ground level, and (b) canopy level. Top ten most abundant taxa at hedge bottom and hedge canopy are shown, as well as the Total abundance for all taxa combined. Explanatory variables: Rain; Wind speed; Humidity; Temperature

(a)



(b)

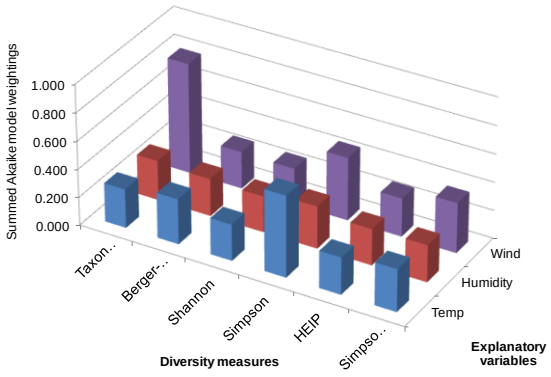


Figure 6.9a-b. Summed Akaike model weights for weather variables potentially explaining invertebrate diversity (Taxon Richness, Berger-Parker, Shannon, Simpson, Heip, Simpson Evenness) at: (a) ground level, and (b) canopy level. All months combined: April, July, September. Explanatory variables: Rain; Wind speed; Humidity; Temperature

Table 6.36a. Best models ($\Delta i \leq 2$) explaining invertebrate diversity in hedgerows at ground level using weather conditions as explanatory variables. Key to weather variables: H = humidity; R = rainfall; T = temperature; WSH = wind speed

Candidate models	k	AICc	Δi	w_i	acc w_i	ER
Taxon Richness						
T	2	22.56	0.00	0.18	0.18	---
Intercept	1	23.01	0.45	0.14	0.32	1.25
R	2	23.79	1.23	0.10	0.42	1.85
T + W	3	23.81	1.25	0.10	0.51	1.87
T + R	3	23.92	1.36	0.09	0.60	1.98
T + H	3	24.41	1.85	0.07	0.67	2.53
Berger-Parker						
T	2	41.63	0.00	0.18	0.18	---
Intercept	1	42.25	0.62	0.13	0.31	1.37
T + W	3	42.25	0.62	0.13	0.44	1.37
T + H	3	42.71	1.08	0.10	0.54	1.72
T + R	3	43.46	1.83	0.07	0.61	2.50
Shannon						
Intercept	1	15.01	0.00	0.24	0.24	---
T	2	16.01	1.00	0.15	0.38	1.65
R	2	16.84	1.83	0.10	0.48	2.49
W	2	17.01	2.00	0.09	0.57	2.71
Simpson (Diversity)						
T + W	3	69.71	0.00	0.29	0.29	---
T	2	70.92	1.21	0.16	0.45	1.83
T + H	3	71.28	1.57	0.13	0.58	2.19
T + H + W	4	71.43	1.72	0.12	0.71	2.36
T + W + R	4	71.71	2.00	0.11	0.81	2.72
Heip (Evenness)						
Intercept	1	12.23	0.00	0.27	0.27	---
T	2	13.71	1.48	0.13	0.40	2.09
Simpson (Evenness)						
Intercept	1	11.53	0.00	0.28	0.28	---
T	2	13.30	1.77	0.12	0.40	2.42
R	2	13.53	2.00	0.10	0.50	2.71

Table 6.36b. Best models ($\Delta i \leq 2$) explaining invertebrate diversity in hedgerows at canopy level using weather conditions (Silva handheld device) as explanatory variables. Key to weather variables: HH = humidity handheld; TH = temperature handheld; WSH = wind speed handheld

Candidate models	k	AICc	Δi	w_i	acc w_i	ER
Taxon Richness						
WSH	2	54.50	0.00	0.40	0.40	---
HH + WSH	3	56.20	1.70	0.17	0.57	2.34
TH + WSH	3	56.33	1.83	0.16	0.73	2.50
Berger-Parker						
Intercept	1	37.32	0.00	0.36	0.36	---
TH	2	38.76	1.44	0.18	0.54	2.06
HH	2	39.28	1.96	0.14	0.67	2.67
WSH	2	39.32	2.00	0.13	0.81	2.72
Shannon						
Intercept	1	10.92	0.00	0.41	0.41	---
Simpson (Diversity)						
TH	2	79.58	0.00	0.23	0.23	---
TH + WSH	3	80.14	0.56	0.17	0.40	1.33
Intercept	1	80.29	0.71	0.16	0.56	1.43
WSH	2	80.61	1.03	0.14	0.70	1.67
TH + HH	3	81.45	1.87	0.09	0.79	2.55
TH + HH + WSH	4	81.46	1.88	0.09	0.88	2.56
Heip (Evenness)						
Intercept	1	11.71	0.00	0.40	0.40	---
WSH	2	13.64	1.93	0.15	0.55	2.63
Simpson (Evenness)						
Intercept	1	18.82	0.00	0.33	0.33	---
WSH	2	19.97	1.15	0.19	0.52	1.78
TH	2	20.48	1.66	0.14	0.66	2.29

Table 6.37. Comparison of the averaged Akaike weightings for weather conditions used as explanatory variables for invertebrate diversity at both hedge bottom and hedge canopy. Values for mean, median, ±SD and ±SE are shown

Analysis - explanatory variables		Akaike Mean (n = 11)	Akaike Median (n = 11)	±SD	±SE
Ground level	**Invertebrate diversity**				
(Sticky traps)	Rain	0.286	0.278	0.035	0.014
	Temperature	0.530	0.468	0.259	0.106
	Humidity	0.285	0.264	0.040	0.016
	Wind Speed	0.340	0.289	0.119	0.049
Canopy level	**Invertebrate diversity**				
(Beating)	Temperature	0.334	0.290	0.123	0.050
	Humidity	0.272	0.265	0.017	0.007
	Wind Speed	0.398	0.315	0.205	0.084

Table 6.38. Results of Kruskal-Wallis tests on differences between the Akaike weightings of weather conditions as candidate variables explaining abundance and diversity of hedgerow invertebrates in the hedge bottom and hedge canopy. Mann-Whitney pairwise post hoc tests are shown for significant results only. Asterisks mark the significantly higher weighted variables

		Kruskal-Wallis				Post hoc tests		
Analysis - dependent variables		**n**	**df**	***H***	***p***	***U***	***p***	
Sticky traps	**Diversity**	6	3	**9.45**	**0.024**	**2.00**	**0.010**	**R v T***
(Ground level)						**3.00**	**0.016**	**H v T***
Beatings	**Diversity**	6	2	2.54	0.281		ns	
(Canopy level)								

Table 6.39. Results of Spearman rank correlations showing the relationship between the diversity of invertebrates in the hedge bottom and temperature. All months combined: April, July, September. An FDR-corrected significance level of 0.02 was applied

Measures of diversity	n	r_s	*p*
Taxon Richness	**95**	**0.388**	**<0.001**
Berger-Parker	**95**	**0.253**	**0.013**
Shannon	**95**	**0.380**	**<0.001**
Simpson (Diversity)	**95**	**0.318**	**0.002**
Heip (Evenness)	**95**	**0.331**	**0.001**
Simpson (Evenness)	**95**	**0.249**	**0.015**

6.4. Discussion

6.4.1. Botanical diversity

Botanical diversity at ground level was an important factor in determining invertebrate abundance at ground level, but botanical diversity measured as Taxon Richness at the individual trap locations (TVTR), not that measured by quadrat (MVTRQ). This suggested that hedge basal vegetation at a very localised scale was better at explaining invertebrate populations than botanical diversity measured by a relatively larger quadrat. Conducting optimal management of the hedge bottom at what might be considered a micro-habitat scale is impractical, but to secure diversity at this level might not require intervention as such. Dunkley & Boatman (1994) even saw merit in non-intervention and suggested more care to avoid application or drift of pesticides and fertilisers into the 2m protection zone.

Botanical diversity in the hedge bottom, rather than the woody/shrubby diversity of the hedgerow itself, appeared to be a relatively important factor also in determining canopy-level fauna. That ground conditions therefore seem to influence canopy populations suggests interchange between the two components of the hedgerow. Joyce *et al.* (1997) looked at arthropod mobility within the hedgerow, but it was unclear whether recolonisation was from the hedgerow only or also from other surrounding landscape features, such as other fields. As noted previously, studies of hedgerow invertebrates tend to separate the two components of the hedgerow, its grassy base and woodier top, with an emphasis on the former. Although there are numerous studies which examine the horizontal or linear interchange/dispersal of invertebrates between (h)edge habitats and adjacent cultivated land (*e.g.* Lewis, 1969b; Varchola & Dunn, 1999; Frouz & Paoletti, 2000; Holland & Fahrig, 2001; Moreby & Southway, 2001), no evidence has been found to suggest that the vertical dispersal between hedge bottom and hedge canopy has been explored. The structural/architectural heterogeneity provided by the variety of different flowering species may be more important than botanical diversity *per se* (Kirby, 1993).

Individual invertebrate taxa from the hedge bottom exhibited a range of responses to botanical diversity. Modelling showed that a combination of both woody taxon richness (WTR) and botanical diversity around the trap site (TVTR) was the best determinant of total abundance. TVTR appeared to be important overall for invertebrate abundance at the base of the hedges, being a component of the top models for all individual taxa, barring Diptera. Diptera were dominated by taxa such as Phoridae, a diverse group which includes nectar feeders, but also fungivores and predators and parasites of other invertebrates, and

Sciaroidea, a superfamily containing many fungus-feeders commonly known as "fungus gnats" (Barnard, 2011). It is therefore perhaps unsurprising that Diptera as a group did not appear to respond to floral diversity. There was, however, no difference between the averaged weightings for the different measures of botanical diversity, suggesting that botanical diversity in the hedge bottom (at least at family-level) and in the woody part of the hedgerow itself were equally important for the abundance of invertebrates overall, notwithstanding differences in responses by individual taxa at ground level.

The correlations between canopy-active invertebrate taxa and TVTR showed that the majority of individual taxa had no significant relationship with botanical diversity at ground level, but that woody taxon richness (WTR) was no better at explaining invertebrate numbers in the hedge itself. It may be that structural elements of the hedgerow were more important determinants of abundance for certain taxa in the hedge tops. For instance, vegetation structure, rather than species diversity *per se*, is known to be a significant factor for web-building Araneae (Maudsley *et al*., 2002). Woody Taxon Richness was also not a prominent factor in the abundance of Psocoptera (barkflies) at canopy level. This might be explained by the fact that Psocoptera, as inhabitants of tree/shrub bark and foliage, and consumers of lichens, algae, fungi and organic 'debris' may not require botanical diversity as such, but are more dependent on structural factors (New, 2005b). Nonetheless, there does appear to be specific host plant dependency as "the greatest diversity and numbers of barkfly species are often found on oak, beech, yew, pine, elder and hawthorn" (BRC, no date). Another potential reason for lack of response to WTR, may be the fact that numbers of woody/shrubby species in the hedgerows probably do not vary sufficiently to provide significant relationships.

For three of the four canopy-active taxa for which a significant correlation was found between botanical diversity and abundance, the relationship is perhaps unsurprising, since the groups Hemiptera, Lepidoptera and Thysanoptera between them contain many herbivores and/or pollinators, which are known to feed on a variety of plants, with many species restricted to certain plant hosts (Barnard, 2011). Certain Acari, although many species are predatory or parasitic, can be plant-feeding, and some groups show plant-specificity, *e.g.* grass mites (Alford, 2011).

Barr *et al*. (2005) reported that numbers of shrubby species were positively correlated with the diversity of invertebrates in a hedgerow. This was not corroborated by the modelling in this study, which showed that WTR was a comparatively weaker model component than measures of botanical diversity in the hedge bottom. Marshall *et al.* (2001)

concluded that enhancing plant diversity at hedge bottom enhanced insect diversity (specifically Heteropteran, rather than the broader assemblage) in a hedgerow. The importance of weeds, such as *Urtica dioica* (Stinging-nettles), to a variety of insects was emphasized. Nettles were a common feature of both Mature and New hedgerows, although more evident in the former than the latter.

The response of invertebrate diversity to botanical diversity at ground level and canopy level was not consistent, and shows that such results can be dependent on the measure or index selected. In terms of the top botanic models, none was better than the intercept-only model for explaining invertebrate diversity in the hedge bottom. In addition, there was no significant difference between the averaged full model weightings for the three measures of botanical diversity, leading to the conclusion that all measures were at best equivalent, at worst 'indifferent' at explaining invertebrate diversity at ground level.

It was unclear why a measure of ground floral diversity (TVTR) was the top explanatory factor for Taxon Richness at canopy level. This may point to the movement of organisms with different host-specificities from hedge bottom into the hedge canopy. The individual responses of Berger-Parker and Simpson indices to WTR were comparatively stronger than to TVTR or MVTRQ and WTR was also the top factor for Heip. The importance of woody diversity to the diversity of life in the hedgerow itself seems intuitively right, is generally acknowledged (*e.g.* Natural England, 2008) and has been shown by previous research (*e.g.* IGER, 2000). Why it was not the top explanatory factor for all diversity indices remains unclear, except that different diversity indices tended to show inconsistent responses to variables. There was no significant difference between the averaged full model weightings for the three measures of botanical diversity, suggesting that they all played a comparable role in determining invertebrate diversity at canopy level.

Asteraki (2004) found that maturity of vegetation (grasses and forbs) in field margins had an effect on plant diversity. Notably, longer established plots were associated with more diverse vegetation, at least over short-term periods, and the diversity and abundance of certain invertebrates was positively correlated with plant richness. Pywell *et al.* (2005) found that vegetation diversity and richness of and cover of forbs increased significantly with age of boundary habitats (hedges and field margins). The results of my study also suggest that herbaceous diversity at the base of the hedge increases significantly with age of hedgerow. Mature hedges showed superior botanical diversity in the hedge bottom, but were often characterised by plants indicating nutrient enrichment, *i.e. Urtica dioica* (stinging nettles), *Rumex* species (docks) and *Galium aparine* (cleavers). Nettles in

particular might be considered undesirable and unsightly in abundance, but are known to be beneficial to insects (Barr *et al*., 2005). Some research indicates that unless re-sown and restored, hedge bases and margins can quickly become dominated by a small number of species, so that herbaceous diversity decreases rather than increases over time (Garbutt & Sparks, 2002; Pywell *et al*., 2011). Hegarty *et al.* (1994), however, found that unmanaged hedges were not as dominated by competitive-ruderal plant species, such as nettles and cleavers, as managed hedges. It is unlikely however that farmland hedges will be taken out of management under AES, since unmanaged hedges may eventually become tree lines and effectively count as a loss to the hedgerow network.

An effect of maturity on plant diversity was not shown for the woody part of the hedgerow and this is likely to be due to the fact that the Mature hedges were dominated by hawthorn (*Cretaegus monogyna*) and the New hedges have generally been planted with a mix of species, albeit retaining a majority of hawthorn. Recommendations to farmers when planting new hedgerows leave room for freedom of choice, although Natural England (2008) suggests using "species that are typical for the local area", acknowledging that these mixes usually contain a majority (60%) of hawthorn and/or blackthorn, or hazel, at least in the South-West.

6.4.2. Ground vegetation structure

Results suggested that taller vegetation was associated with higher numbers of invertebrates. Maximum sward height (MSH) had a greater full-model weighting than other explanatory factors, but there was no statistically significant difference between MSH and the other variables. While Morris (2000) found that tall grassland supported more individuals and a greater diversity of arthropods than short swards, a varied structure, both on a larger and smaller scale, is deemed to be crucial (Kirby, 1993). Different taxa will have different spatial distributions and requirements (Maudsley *et al*., 2002). It is likely that many different, natural and man-managed, features of habitat interact in creating beneficial variety and complexity to meet these requirements. Height of vegetation will be one factor in providing shelter, for instance, while other characteristics, such as density of vegetation *etc* will also be important.

For invertebrate abundance at canopy level, ground light levels (GL) were the key factors determining invertebrate abundance in general. As light penetration at ground level increased so the numbers of invertebrates generally decreased. Since GL is determined partly by the density of vegetation (and also probably height of sward) in the hedge bottom, but also by the density of the hedge canopy foliage above, it could be regarded as a

proxy for directly measured vegetation density and by extension the sheltering capability of the hedgerow. Invertebrate activity and dispersal may have increased where the canopy vegetation was sparser, letting more light penetrate to ground level.

Sward height (MSH), not GL, was the key factor for Psocoptera or Thysanoptera in the hedge top. Reasons for this are unclear, but might suggest some interaction between the hedge bottom and hedge top for these taxa. It is possible that sampling by the beating technique used may have captured specimens in a 'transitional' zone where the tall sward met the canopy. Psocoptera are typically arboreal but Alexander (2011) indicates that a few species are also supported by tall grassy vegetation, and although associated mainly with bark, some are predominantly found on foliage. In the case of Thysanoptera, many species are associated with wild and cultivated grasses as well as a variety of different flowers and fungi, can be hidden beneath leaf litter and bark (Barnard, 2011), from where they migrate to host plants (Alford, 1999).

For invertebrate diversity at ground level MSH was the most important factor overall, suggesting that the taller the vegetation, the more diverse the invertebrate assemblage at the hedge bottom. De Cauwer *et al*. (2006) have shown that insect diversity can be significantly greater in shaded areas of field margins and relates particularly to taxa preferring moist conditions, including Diptera such as Sciaroidea and Cecidomyiidae noted in this study (Chapter 4). Pywell *et al.* (2005) indicated that basal vegetation, which has been allowed to grow tall, can benefit overwintering predatory arthropods by providing 'insulation' from winter weather conditions. The sheltering function of hedgerows consists of providing stable refuges from agricultural disturbance, breeding sites, food resources and corridors for dispersal (Pywell *et al*., 2005). A sheltered hedge base, such as that provided by longer vegetation, promotes higher densities and richness of Coleoptera and Araneae (Pywell *et al.*, 2005). Pywell *et al*. (2011) also recognised that tall vegetation provides shelter and nesting sites, which could be complementary to wildflower habitat. Work by the RSPB (2012b) in its London House Sparrows Parks Project indicates that long grass is very highly beneficial to invertebrates (and therefore chick food), increasing abundance greatly compared with short grass controls. This was to an even greater extent than wildlife seed mix treatments (of the type used under Stewardship agreements). Long grass was also far less expensive and easier to manage than either wildflower or wildlife seed treatments.

Regarding invertebrate diversity in the hedge canopy, MSH was especially important to Simpson (diversity), Berger-Parker and to a lesser extent Taxon Richness.

Responses to structural variables were fairly uniform for other diversity measures. Sward height was also the key factor in top models explaining canopy assemblage diversity by most measures, although Margin Width (MW) appeared to be important for Simpson (diversity). Again, it is tempting to see the importance of sward height as perhaps suggestive of 'interchange' of invertebrate populations from hedge bottom, which could be influenced by the fact that high vegetation in the sward can often meet the canopy thereby forming a transitional zone. There was, however, no significant difference between the weightings of the respective full model components and therefore in terms of explaining invertebrate diversity in the hedge canopy structural variables at ground level were of equivalent power.

Overall, results from the analysis of structural aspects of ground vegetation serve to underline the fact that spatial complexity is composed of a variety of different elements, to which invertebrate taxa will respond differentially and, which are not easy to pick apart. Furthermore, since there was no significant difference in these structural elements between Mature and New habitats, the key to maintaining important structural benefits of the ground vegetation is less a question of age than management intervention. Planting hedges and thereby creating a theoretically protected strip of non-crop habitat would seem to relatively quickly enable conditions of structural complexity to arise/be created equivalent to more established hedgerow habitats.

6.4.3. Hedge structure

Although measures of canopy height (and thereby volume) were important in top models of invertebrate abundance at ground level, canopy light (CL) was overall the key explanatory variable in the hedge bottom as well as the canopy. The relationship between light conditions and the abundance of taxa was largely negative; therefore, the higher the density of vegetation (branches, foliage and fruits) in the woody part of the hedgerow (and therefore the lower the light levels), the higher the numbers of invertebrates found in both the hedge bottom and hedge top. Numbers of Psocoptera in the hedge top had the strongest negative relationship with CL, in keeping with the requirement for 'cryptic' conditions and rather sedentary lifestyle of this Order. Psocoptera are largely arboreal and most species found on bark, although some on foliage (Alexander, 2011), therefore dense vegetation would presumably be preferred. Amy *et al*. (2015) found that higher Psocoptera abundance was associated with less variability in gappiness of the hedge canopy, suggesting a preference for a more closed and clumped (*i.e*. fundamentally denser) canopy. Canopy Light was however not a key correlate for all taxa: the abundance of Coleoptera,

Diptera and Thysanoptera had no significant relationship with CL at either ground level or in the canopy. This might indicate readier ability to disperse or a preference for more open habitat.

Canopy light was also the leading model component in accounting for the diversity of invertebrate assemblages at the base of the hedges as well as in the hedge tops. Nonetheless, whereas CL was a significant factor for diversity in the hedge bottom, its averaged weightings were ultimately not significantly different from other candidate variables explaining diversity in the hedge canopy. The reasons for this are unclear, other than to observe that a denser canopy presumably contributes to shadier conditions at ground level which are known to support more diverse insect populations (De Cauwer *et al*., 2006). Shade at ground level would help ensure damp conditions and a denser canopy may well produce and retain greater amounts of leaf litter, all of which would encourage a diversity of organisms that may not thrive in the canopy. A range of features contribute towards critical structural variety (Kirby, 1993) and sheer volume (as measured by height and width) also has a part to play in providing space in which invertebrates may "find a living" (Kirby, 1993), providing a greater surface area available to organisms for feeding, resting and egg-laying than sparser vegetation.

Irrespective of the density of the canopy, there are also other factors which affect the relative vagility of populations in the canopy, such as unsteady air turbulence around branches and stems, which has the capability of affecting foraging behaviour in flying insects (Ravi *et al.*, 2013), or simply greater exposure to weather. Commentators have observed the relative lack of abundance and diversity of arthropods in the canopy environment which is independent of sampling effect: the general pattern of higher abundance (and richness) of temperate forest arthropods near to the forest floor has been explained by a number of factors, including the greater stability of the microclimate nearer to the ground (Parker, 1995), availability of refuge from natural enemies and the distribution and quality of food resources (Aikens *et al*., 2013).

Density of hedgerow vegetation is presumed to be important in providing shelter for a range of invertebrates. Indeed, the sheltering qualities of farmland hedgerows are well-acknowledged, forming reservoirs of both pest and predator taxa (*e.g.* Buglife, no date), particularly of mature hedges (Pollard, 1968b). With regard to age-dependent effects, no significant difference was found between the densities of the Mature and New hedges, although there were significant differences in measures of height and width. Interestingly, Lepidoptera were the only taxon whose numbers showed a significant

response to both height and width of the hedge top, suggesting that the larger dimensions associated with Mature hedges (which were significantly taller and wider than New hedges) were important for butterfly/moth populations. Taller hedgerows can support increased butterfly species richness (Barr *et al*., 2005). Numbers of Hemiptera were also significantly correlated with height, though not width, which suggests that larger Mature hedges would harbour greater numbers of bugs. Suppressing the size of an arable hedge through management might seem a desirable aim in order to contain potential crop pests such as aphids, but Hemiptera are a diverse group containing predatory as well as herbivorous species (Chinery, 2007; Barnard, 2011).

For Coleoptera and Araneae width and height of canopy were more important factors than canopy light both at ground level and in the hedge canopy. This indicates better dispersal capability compared with other taxa and may reflect avoidance of dense vegetation which could impede movement. Araneae responded particularly well to growth in height, suggestive of an ability to exploit spatial volume, if not complexity, during the growing season. Spiders are known to respond well to, if not require, habitat complexity, in particular web-building species (Foelix, 1996; Agnarsson, no date). Diehl *et al*. (2013) indicated that reduced management intensity and increased vegetation complexity help conserve invertebrate diversity and that cutting can have a negative effect on the communities of spiders and their prey. It was perhaps surprising that neither hedgerow height nor width appeared to have a stronger effect on abundance and diversity, since these measurements are indicative of the hedgerow volume, and thereby the potential living space available to wildlife. Maudsley *et al.* (2002) also noted a 'surprising' lack of significant relationships between measured habitat variables (including hedge width and height) and arthropod numbers.

Taller hedgerows can benefit invertebrates by increasing species diversity (Barr *et al*., 2005). Indeed, Hooper (1992) recommended that the ideal hedge should be 4m high and 4m wide and unmanaged. Dover *et al.* (1997) however suggested that for butterflies at least hedge density, and the shelter it confers, is more important than hedge height. In fact, being tall and wide, characteristics of more mature hedgerows, may even suffer sparsity of vegetation and loss of density through lack of management (or mismanagement) over time, thereby negating the sheltering effect. Currently, the loss of hedgerows and their degradation to remnants is thought to outweigh losses through direct removal (Staley *et al*., 2012a). Therefore, increased AES funding and more widespread availability of options for rejuvenation of hedgerows through management techniques, such as laying and new

planting, have been called for by Hedgelink (Wolton, 2011). Recent changes to AES options and payments may be addressing the lack of investment in hedgerows through Higher Tier and Mid Tier Stewardship and Capital Grants (Natural England, 2015).

According to Kirby (1993), "the importance of varied vegetation structure cannot be overstated" and may be independent of stage of growth. While ecological studies of vegetation have observed increase of complexity with age (*e.g*. Munro *et al*, 2009, over 30-40 years), in fact, complexity may ultimately decrease over time and loss of complexity with senescence has been observed as a general physical/physiological and mathematical phenomenon (Lipsitz & Goldberger, 1992). To explore the connection between age and complexity further in the case of hedgerows could involve more detailed image analysis, through the use of high quality digital (hemispherical) photography such as that undertaken in canopy studies and an image analysis application, such as ImageJ. Similar work has recently been done to explore the effects of management treatments on hedgerow gappiness (Amy *et al*., 2015), which indicated that less variation in gap size positively influenced the diversity of herbivorous taxa and the abundance of detritivores such as Psocoptera and Collembola in the canopy. Conversely, studies from forest ecology have suggested that heterogeneous openings in woody habitats, caused by natural processes over time, encourage taxa such as pollinators (Bouget & Duelli, 2004).

6.4.4. Landscape context

For invertebrate numbers at ground level, geographical location (L) was overall the key explanatory factor identified, but by no means for the majority of taxa. Hedgerows at Swallow seemed to harbour comparatively greater numbers of Isopoda, Hemiptera, Thysanoptera and Opiliones, whereas hedgerows at the three other sites harboured one or two other taxa in abundance. The reasons for the differences in sites are uncertain: the most obvious differences were a marginally greater concentration of cereal crops and a higher frequency of Mature hedge habitats at the Swallow site than elsewhere. Despite this, location did not appear to affect the total abundance of invertebrates and also for some individual taxa location made no difference to their numbers. The non-responsive taxa included a number of flying insects, notably Hemiptera and Hymenoptera, with presumably good dispersal ability, but also Araneae. In the case of Araneae, dispersal may be achieved by 'ballooning' which means they can 'fly' by being carried on the wind (Jones-Walter, 1989), but obviously lack the control of truly flying insects. By contrast, Diptera did respond to location and this may have to do with the fact that many of the types

of flies caught were essentially weakly flying and not strong dispersers, such as fungus gnats and phorid flies, known to 'scuttle' (Barnard, 2011).

Alongside location, distance from woodland (DW) was also identified as a comparatively important factor for ground-occurring invertebrates, but ultimately only Opiliones was significantly positively correlated with DW. Although harvestmen are often associated with damp woodland (Hillyard, 2005), they do not seem to rely on wooded areas and can occur in any shady, damp place, and can also inhabit more open habitats such as grasslands (Richards, 2010). Indeed, Opiliones were more abundant in the grassy hedgeless boundaries than in the hedge bottoms. The findings fit with those of Sotherton *et al*. (1981), who found that harvestmen preferred remnant hedges (more open areas) to managed hedges. Half the individual taxa increased as distance from woodland (DW) increased, but this association was always weak to very weak, also for the remaining taxa whose numbers decreased as DW increased (notably Araneae, Coleoptera and Diptera). Nonetheless, correlations with DW might suggest the presence of forest species for which hedgerows, although not true woodland, may provide some extensive woody habitat in otherwise steppe-like arable eco-systems. Dennis (1997) certainly thought of hedgerows as emulating a woodland-type microclimate for insects. Fischer *et al.* (2013) found that forest species of spiders and Carabid beetles were more likely to occur in forest edges than farmland hedges, but that some generalists (beetles but not spiders), and species associated with more open habitats, were more abundant in hedges than forest edges.

Connectivity (C) and DW were weighted higher than location for invertebrate diversity at the base of the hedge. Correlations showed that there was however no significant statistical relationship between diversity (of any measure) and distance from woodland or connectivity. Therefore, an increase in the overall diversity of the invertebrate assemblage with an increase in 'connectedness' with woody habitats could not be shown, despite research suggesting beneficial effects, at least for certain taxa. The importance of connectivity in landscapes to form dispersal corridors for invertebrates, even woodland specialists has been suggested by research on Carabid beetles and butterflies (Barr *et al.*, 2005; Burel & Baudry, 2012). Where hedgerows have been planted closer to woodland, perhaps organisms inhabit the woodland in preference to the hedgerow? On the other hand, where there is no choice, further away from woodland, the variety of invertebrate organisms associated with hedges could be generalists, open-habitat specialists or sub-populations of forest species capable of adapting to the smaller woody environment of hedgerows. Merckx & van Dyck (2007) found a certain amount of adaptive behaviour

amongst Speckled Wood butterflies (*Pararge aegeria*), with some able to cope better with habitat fragmentation than others, and those of woodland origin being less adept. Generally, however, the requirement for successful adaptation by Speckled Woods was tall hedgerows and trees, of the type seen in more Mature hedges. Martin *et al.* (2001) suggested that the forest Carabid species *Abax ater* was "not able to discriminate between dense hedgerows and woods", but this might not be true of other taxa. Krewenka *et al.* (2011) examined effects of large hedgerows on the foraging and dispersal ability of Hymenoptera, and found that for bees and wasps small-scale (< 750 m), localised connectivity and a corridor effect may not be important.

For both invertebrate abundance and diversity at canopy level, the most highly weighted factor was DW, but statistically it was no better at explaining canopy-active invertebrate abundance and diversity than connectivity or location. The latter appeared to be comparatively important for Taxon Richness, but again this was not a statistically significant response. The highest Taxon Richness at ground level was associated with Riseholme, where the area surrounding the arable fields was more varied than at other sites, encompassing pasture, woodland, a lake and horticulture, whereby heterogeneity of the local landscape was presumed to be a factor: simplification of agricultural landscapes is implicated in biodiversity loss (*e.g.* Benton *et al*., 2003). That the diversity of hedge canopy fauna seems relatively less affected by landscape context than invertebrates of the hedge bottom may reflect the mobility and range-size of canopy organisms. Moreover, the canopy fauna in this situation could embrace large numbers of flying visitors or 'tourist' taxa with good dispersal ability.

6.4.5. Weather

As rainfall increased the abundance of all taxa in the hedge bottom increased significantly, with the exception of Collembola and Opiliones. Total abundance of all taxa was highly significantly correlated with rainfall. This perhaps indicates shelter-seeking behaviour driving up populations during inclement weather in surrounding farmland. Reasons why numbers of Collembola and Opiliones are not strongly correlated with rainfall are unclear, since both taxa prefer moist conditions (Coleman *et al*., 2004; Hopkin, 2007; Richards, 2010). Rain (and wind) can affect invertebrate taxa differently: while rain and wind can aid dispersal of some small insects, it can inhibit the activity of others or dislodge them making them vulnerable to attack by predators (Alford, 2011).

Numbers of the majority of individual taxa were significantly positively correlated with temperature, or had a relationship approaching significance. This is also likely to

reflect a general rise in invertebrate activity as temperatures become warmer. Araneae was the only taxon whose relationship with temperature did not even approach significance, perhaps indicating that other factors, such as vegetation structure, outweigh the influence of weather. Only Collembola was significantly negatively associated with temperature, with numbers decreasing with increases in warmth. Collembola are recognised as being particularly intolerant of water loss (Coleman *et al*., 2004), so perhaps dessication avoidance is important here. Their preferred 'thermobiological' range varies depending on species, but some species are markedly more active at lower temperatures (Hopkin, 1997).

For canopy level abundance the key explanatory factor for total abundance and the majority of individual taxa was Wind Speed (WSH) at the time of collection. This is unsurprising given the greater exposure of higher vegetation to the elements. Indeed, the canopy of a hedgerow, like those of forest canopies, is where "biodiversity meets the atmosphere" (Ozanne *et al*., 2003). Even low wind speed and gentle air movement will affect the numbers of invertebrates and their presence or apparency in the hedge canopy, since they may be carried away or take shelter elsewhere (Pasek, 1988; Alford, 2011). Maudsley *et al.* (2002) found that shelter from wind was an important factor influencing the abundance of spiders in hedge foliage and identified hedge orientation, prevailing wind direction and hedge vegetation as key. Although sampling of canopies was generally avoided in breezy conditions, at least some air turbulence associated with woody habitats is inevitable (Ravi *et al*., 2013) and likely to affect composition and abundance of catches.

Although the full model weighting of WSH, averaged for all diversity measures, was the highest of the three variables, there was no significant difference between its explanatory power and that of the other variables. In addition, diversity indices did not respond consistently to the weather variables: WSH was a determinant of Taxon Richness, but was not so important for any other measure. Conversely, Simpson diversity responded more strongly to temperature (TH) than wind speed (WSH) or humidity (HH). The reasons for this are unclear but may be to do with the way in which Simpson is calculated, which can exclude single representatives within the sample.

Although the variety of effects of temperature, wind and rain on the ecology of insects generally is recognised (Speight *et al*., 1999), evidence is confined largely to single taxon studies and information on farmland hedgerow systems is sparse, although research has for instance shown variously effects of windbreak and a sheltered microclimate. Lewis (1969a) found greater numbers of insects near hedgerows during windy weather than calm conditions, attributing this to a windbreak effect, but also indicating that wind leads to

disturbance of populations from localised sheltered vegetation. Microclimatic conditions, such as elevated temperature and humidity in hedgerows, can be important, *e.g.* to farmland butterflies (Barr *et al*., 2005). They are influenced by larger-scale climate and can differ by some degrees from measures of ambient conditions, such as those used here. By contrast, Ulrich & Fiera (2009) investigated the environmental correlates of Collembola diversity at a large geographical scale and found that area, winter length and annual temperature range (as opposed to the shorter term temperature measures taken in this study) were major predictors of species richness. In order to bolster assertions made about the sheltering effects of hedgerows also, this study could have benefited from an exploration of more detailed microclimatic and weather data over longer periods.

Barr *et al*. (2005) indicated the importance of the protection from extremes of climate provided by hedgerows to invertebrates generally. Even the much-prized sheltering effect of the hedgerow, could however be neutralised by the power of the weather. There is much discussion surrounding the impact of global warming on weather patterns: changes in rainfall patterns are likely to affect flight period, food availability, may cause direct mortality (*e.g.* through droughts and flooding) and result in significant changes in habitat quality (Mossman *et al*., 2013). In the UK we usually consider ourselves lucky to enjoy a climate that is not too extreme. Increasing extreme weather events even here could nonetheless cause damage and bring disease to the woody and herbaceous parts of the hedgerow, changing the composition of hedgerow wildlife (Natural England and RSPB, 2014) and interfering with the apparency or survival of invertebrate taxa. Ewald *et al*. (2014) indicated differential effects of extreme weather on 28 invertebrate groups commonly found in cereal crops, with good short-term recovery of the majority of taxa, but 'likely' long-term effects of climate change on abundances of some. The long-term effects on hedgerow invertebrates of predicted decreases in summer rainfall and increases in temperature and winter rainfall are also likely to be contrasting, but as yet unknown.

6.4.6. Conclusion

This study showed mixed responses to the different explanatory variables, but that in general measures of vegetation density (which might be considered proxies for 'shelter' and structural complexity) were positively correlated with the numbers and diversity of hedgerow invertebrates in both the hedge bottom and canopy, supporting previous research (*e.g.* Maudsley *et al.*, 2000). There was no difference between the respective densities of New or Mature hedges and it appears that both would therefore be capable of providing valuable shelter to a variety of invertebrate taxa, from the unstable conditions inherent in

agro-ecosystems (Alford, 2011). The particular association of Psocoptera with denser vegetation is interesting in view of the findings of Amy *et al.* (2015), regarding the association of higher abundances of detritivores, including Psocoptera, and higher diversity of herbivores with lower variation in canopy gap size. It suggests that for some taxa at least more homogeneous conditions offering consistently good shelter may be a factor.

Given the emphasis placed on the importance of vegetation structure to invertebrate populations, it was perhaps surprising that structural dimensions of the hedge itself, notably height and width were not more strongly correlated with invertebrate abundance and diversity. Sheer volume is however no guarantee of structural diversity or complexity, which is a requirement for good invertebrate habitat (Kirby, 1993).

It may be that some refinement of data collection would be necessary to explore these points further. Measured structural variables such as canopy density and complexity could have been improved with image analysis, such as that conducted by Amy *et al*. (2015). In particular, the estimates of ground cover may be unsatisfactory, due to the reliance on a visual estimate based on % bands. Use of hand-held, readily portable (but costly) equipment, such as Decagon's AccuPAR LP-80 which calculates canopy photosynthetically active radiation (PAR) and leaf area index (LAI) would give a greater level of detail.

Botanical diversity did not appear to be as strong an influence as other factors overall, perhaps reflective of the presence of generalist rather than host-specific taxa, and predatory taxa, in the assemblage. Many invertebrates, including rare species, feed on common plants (Kirby, 1993), therefore a lack of botanical diversity may not be critical as such, although diversity of plant species (as well as a mix of ages) will contribute to the structural diversity of vegetation, which is seen by some as of overriding importance (Kirby, 1993). Southwood *et al.* (1979) showed that insect diversity was more closely related to plant architectural diversity and spatial diversity combined than to plant taxonomic diversity. In this study, the sheer dimensions of the hedgerow in terms of its height and width (characteristic of Mature hedges) were important to few taxa, notably Lepidoptera, whose populations presumably benefited from larger volume – and increased living space – although not necessarily structural complexity/heterogeneity. Invertebrates can exploit very small patches provided the right conditions are present (Kirby, 1993), so in fact smaller habitats may harbour surprisingly great abundance and smaller New hedges need not necessarily be any less preferred than larger Mature hedges. Interestingly, there was no apparent age-dependent effect on light levels/vegetation density at ground level or

in the canopy, suggesting that shady conditions which have been shown to support an abundance and diversity of insects (De Cauwer, 2006) are achievable in the relative short term by planting new hedgerows and establishing a protection zone, even if structural complexity and botanical diversity may take some time to acquire (Munro *et al*., 2009).

Results suggest tall vegetation in the hedge bottom should be maintained and that the density of the hedgerow canopy should be maintained to support invertebrate populations. Having said this, simply leaving tall swards, as some of the findings suggest, might be difficult where hedgerow management is often motivated by a need to preserve farm tidiness (Britt *et al*., 2011). Maintaining or improving density might also require a change in management. For instance, light annual trims are far more likely to produce denser canopies, than the minimum two and three year cycles advised under environmental stewardship (Wolton, 2007; Staley *et al*., 2012b). Annual trims are currently advised for the first 10 years of the life of a new hedgerow under AES, but more mature hedges could also benefit. Leaving hedges uncut for longer periods, such as the three years, can increase berry crops (Staley *et al*., 2012b), but can be unpopular with farmers and their contractors, some of whom prefer an annual trim (Britt *et al*., 2011). Laying is also designed to restore hedgerows and thicken them out, but in the short term destroys structure rather than enhances it. Encouraging the thickening out of vegetation in this way may benefit other species such as farmland birds, by enhancing protection from predators and increasing foraging areas.

Ultimately, the key to creating favourable conditions for farmland invertebrate assemblages will be to maintain heterogeneity of hedgerow habitats of different ages and different levels of management both in the hedge bottom and hedge top. Heterogeneity is recognised as important to population stability (Oliver *et al*., 2010). New plantings, different AES cutting regimes, restoration through laying and coppicing, and also areas of reduced- or non-intervention are all desirable in the admixture. Griffiths *et al.* (2007) emphasized the importance of preserving hedgerow habitat heterogeneity in agro-ecosystems, including “features currently considered of limited conservation value”, such as apparently degraded relict or remnant hedgerows. Further ‘buffering’ of hedgerows, using grass, low intensity management *etc.* to enhance their sheltering qualities and protect them from the impacts of adjacent land use may be desirable (Natural England and RSPB, 2014). Maximising the potential of hedgerows as wildlife habitat will become increasingly important as pressures on farmland intensify – from housing development to food- and energy security and potentially devastating climate change.

Chapter 7. General Discussion and Conclusions

7.1. Effects of hedgerow maturity on the invertebrate assemblage

The relationship between maturity and invertebrate abundance and diversity was not entirely as hypothesized and although the understorey of the hedgerows showed a beneficial effect of maturity on the invertebrate assemblage at ground level, the hedgerows planted as agri-environmental improvements showed no difference in the woody part of the hedgerow (Bennett *et al*., 2013).

7.1.1. Effects of hedgerow maturity on invertebrate abundance

Results from sampling of both the hedge bottoms and hedge canopies indicated that overall the invertebrate abundance of hedgerows newly planted under AES (<15years) was comparable with that of more mature hedgerows (>50 years), *i.e.* there were no significant differences between the hedge age groups on the basis of total abundance of all taxa, although there were some marked differences amongst individual taxa. In addition, at ground level there was no significant difference between the overall invertebrate abundance of hedgerow (either Mature or New) and hedge-free boundaries. For some taxa, a hedgerow would not necessarily be favoured habitat. The presence of well-dispersing open-habitat species on farmland may help explain the similarity in abundance between the hedge age types, as observed with regard to ground beetles and other epigeal arthropods (*e.g.* Gruttke, 1994; Gruttke & Kornacker, 1995). In addition, there are evidently species whose ability to disperse has been underestimated, or which have changed behaviour in response to habitat fragmentation (*e.g.* Chapman *et al*., 2005). Some taxa are reportedly better-adapted than others behaviourally and ecologically to the disturbance and ephemeral conditions prevalent in agro-ecosystems, particularly in farmland dominated by cereals (Ewald *et al*., 2014).

Within both the ground- and canopy-occurring assemblages there were significantly differing responses by individual taxa to hedgerow maturity. A small number of taxa responded more favourably to the Mature hedge bottom (Dermaptera, Isopoda, Julida, Psocoptera and Thysanoptera). The presence of these orders in any number is likely to reflect the presence or vicinity of ageing and decaying plant material, including rotting wood, certain fungi on tree bark and superior opportunities for concealment under leaf litter or bark, all of which might be expected to be provided by more mature habitats. The ground-level conditions of newly-established hedges were apparently preferred by

Hymenoptera (dominated by Formicidae). Araneae and Hemiptera were more abundant in the Hedgeless boundaries, indicating a preference for more open habitat. In the canopy, the abundances of a small set of taxa were significantly affected by Mature hedges (Acari, Hemiptera, Lepidoptera), whereas Pulmonata were found to respond significantly better to New hedges. The reasons for this are not entirely clear, although in the case of snails might have to do with the younger hedgerows being smaller in stature and canopies being more readily accessible from the ground by snails. On the other hand, more mature hedges tending to be larger with greater areas of foliage and woody plant material support larger populations of herbivores (Hemipteran fauna was dominated by aphids, psyllids, leaf- and froghoppers) or may better shelter more cryptic, shade-seeking or delicate organisms, such as moths and their larvae (which dominated the Lepidoptera).

Correlations with hedgerow age in years did not necessarily corroborate the findings from the GLMs based on the binary Mature/New typology. Abundance in the hedge bottom was positively correlated with hedge age in years for the majority of taxa, although only for 4 taxa was that relationship significant (Coleoptera, Diptera, Psocoptera and Thysanoptera). Further examination of Coleoptera and Diptera showed that Mature hedges had consistently higher numbers of family groups than New hedges or hedge-free boundaries (Chapter 4).

Of the invertebrates sampled from hedge canopies, Araneae and Opiliones were the only taxa for which numbers showed a significant correlation with age in years, rather than maturity 'type'. The relationship between abundance and age was negative, showing a decrease in abundance with increasing age. This was the case for the majority of taxa, albeit at a non-significant level, implying that maturing hedgerows may not represent optimal habitat for large parts of the assemblage. The absence of a relationship between age and abundance is likely to reflect not only the difficulties with ageing hedgerows accurately, but also that age is not necessarily a linear process. The maturing of hedgerows is subject to a degree of 'disruption' in agro-ecosystems, through a combination of management and adjacent land use. Although it was clear that mature hedgerows were favoured by certain individual taxa, no precise predictions could be made as to how invertebrate assemblages in the hedge canopy may change over time in response to increasing maturity. A high degree of variability year-on-year has been demonstrated in woodland canopy studies: for instance, Floren (2008) observed that oak communities differed in their order-level composition greatly between consecutive years (2001/2002). As such, these findings therefore provide a snapshot of conditions in the shorter term.

Interpretation of what was found was hampered to an extent by the lack of any comparable studies focused on the canopy of the hedgerows. Some similarities with faunal assemblages were found in other short-term studies of farmland hedges (*e.g.* Joyce *et al.*, 1997; Pollard & Holland, 2006; Amy *et al.*, 2015), which might suggest that the abundance and diversity seen in this study are not entirely atypical of arable farmland hedgerows at a wider geographic scale.

My results reflect diverging responses amongst invertebrate taxa and help illustrate how difficult it is to optimise AES options towards many taxa simultaneously (Gottschalk *et al.*, 2010), particularly a group as vast as the invertebrates. It is therefore perhaps unsurprising that evidence is for AES delivering rather modest benefits to biodiversity, if at all (Kleijn & Sutherland, 2003; Whittingham, 2007, 2011; Boatman *et al.*, 2008, 2010, 2013; Kleijn *et al.*, 2011). McKenzie *et al.* (2013) also pointed to the complexity of the relationship between biodiversity and AES, concluding that collaboration at landscape scale would confer greater benefits on biodiversity.

7.1.2. Effects of hedgerow maturity on invertebrate diversity

Although numbers of ground-occurring invertebrates were comparable between the hedges and the hedgeless boundaries, measures of diversity differed depending on type; Mature hedges exhibited significantly higher diversity than either New hedgerows or Hedgeless boundaries at ground level. New hedges might contribute quickly to the abundance of invertebrates, but acquisition of comparable diversity would seem to take some time. Only a binary distinction between 'Mature' and 'New' was made in the GLM, although certain broad characteristics were identified. Any more precise prediction of how diversity in the hedge bottom might grow or change with the ageing process was not possible. Longer-term monitoring would be required to determine this. By contrast, in the canopy there was no significant difference in diversity between New and Mature hedges, suggesting that young hedges can relatively quickly acquire characteristics of more mature habitats: in this case, AES-funded hedgerow plantings of an average age of ~10 years were no less diverse than considerably older hedgerow habitats. Multivariate analysis suggested that structural features of the hedgerows were a strong factor in this. Indeed, research suggests that conditions favourable to a broad assemblage may be achieved over a relatively short timeframe: Munro *et al.* (2009) indicated that ecological restoration of woody habitats could achieve similar structural complexity to older habitat in 30-40 years.

Invertebrate diversity was significantly affected by hedge age at ground level, with Mature hedges showing higher diversity overall, but in the canopy beatings of equivalent

areas with equivalent intensity showed no difference between the respective hedge age groups. As the Mature hedges generally had a greater hedge volume, it is however possible that higher invertebrate abundance/diversity would have been detected with further sampling (Southwood & Henderson, 2000). The invertebrate abundance and diversity found in New hedges may be limited by the smaller volume of younger hedgerow canopies. In species-area relationships larger islands (in this case a hedgerow could be considered a habitat 'island', ignoring considerations of connectivity), tend to harbour greater numbers of species (Speight *et al*., 1999), but it is also possible for smaller 'islands' to have more species than a larger one. It is therefore not impossible that a smaller relatively newly planted hedge could prove to be more diverse than a larger well-established one, particularly if the latter had been unsympathetically managed. Speight *et al.* (1999) for example indicate that early succession tends to produce higher plant species richness than mature habitats closer to climax, and may therefore have higher insect diversity.

It is also possible that because of the high level of analysis, differences between the diversity of Mature and New hedgerows may have been effectively 'dampened down'. An analysis at a lower taxonomic level (family/superfamily) of Coleoptera and Diptera revealed divergence between the two age groups, although insufficient to draw any statistically significant conclusions. There were many groups common to both hedge age types, but that there was greater beetle and fly family richness in Mature hedges at ground level in every month, but not in the canopy.

7.2. Relationships with other studies on effects of habitat restoration/maturity

My findings correspond broadly with other research into the effects of different types of habitat restoration on wildlife, which has shown evidence for growing maturity having a beneficial effect on invertebrates, and has also highlighted the value of comparatively immature habitats. Meek *et al.* (2002) showed that sown margins could rapidly produce 'substantial' biodiversity benefits to a range of invertebrates on arable land, even within the first season. Floren (2008) showed that the most mature forest canopies ('primary' or ancient) were not necessarily superior in terms of arthropod abundance to much younger forests and in fact the youngest trees (8 years) seemed to be preferred by certain taxa, notably Hymenoptera. Hollier (2008) noted that the abundance of Psocoptera increases with age of field plots and availability of tussocks. Pywell *et al*. (2011) found significant effects of vegetation maturity on the abundance and richness of key invertebrate functional groups in restored field margins over a 3-year period (after

initial sowing), *i.e.* relatively quick gains for new boundary habitats. There were, for example, significant increases in abundance and richness of detritivores across all treatments over the three years "as vegetation communities matured". Twiston-Davies *et al.* (2011), reporting on the Stonehenge Landscape Restoration project, challenged the assumption that it takes 'decades' to reach the ecological conditions of the target habitat. Focusing on benefits to Lepidoptera, they showed that restored grasslands "could approach the ecological conditions of the target chalk grassland habitat within 10 years". They found a correlation between age of habitat and diversity: established chalk grassland exhibited higher Lepidoptera densities than either adjacent restored 'matrices' or arable land, although even 1- or 2- year-old restoration potentially reduced habitat fragmentation. Certain specialist species were absent from the restored habitat, indicating that more generalist species were quicker to take advantage of the restored habitat. Driessen *et al.* (2013) compared new and old re-growth of moorlands after fire and found that invertebrate assemblages did not differ between young and old re-growth. This fits with the similarity between Mature and New hedgerows seen in terms of overall invertebrate abundance and diversity in my study.

Research relating directly to hedgerow planting shows varying effects of age and varying opinions on how long such hedgerows take to provide benefits to invertebrate populations, with some studies indicating longer periods and others suggesting the process is much quicker. While Kromp (1999) found newly established hedges supported more ground beetles than older hedges, Gruttke & Kornacker (1995) studied the development of ground-active invertebrate fauna in young hedge plantations over a period of 9 years, concluding that this was insufficient time for a hedgerow to develop a 'typical' arthropod fauna. They indicated that new hedges develop only 'very slowly', basing their conclusion on the assumption that a mature hedge should resemble mature woodland. The success of the new plantings was judged based on colonisation by a variety of woodland invertebrate species, notably Araneae, Carabidae and Opiliones. They cautioned that taxonomic groups may behave very differently to the same environment and effects shown for certain taxa may not be valid for another. My results based on a broader spectrum view of invertebrate diversity would suggest the process of colonisation or exploitation can be quicker. Even relatively immature hedgerows created through AES were seen to provide support for invertebrate populations from an early stage at both ground level and canopy level, with assemblages closely resembling more mature habitats. Inspection of Coleopteran and

Dipteran families also indicated broadly similar assemblages and dominance by certain groups in both Mature and New hedges.

My findings are consistent with evidence that even immature hedgerows can have an important role to play in supporting invertebrate abundance and diversity in agro-ecosystems (*e.g.* Lechner, 1991; Bergthaler, 1996; Pywell *et al.*, 2005). Pywell, *et al*. (2005), for instance, found that the maturity of hedge and field margin habitats was important to a few species of overwintering spiders and beetles on arable farmland, but was not a decisive factor overall in determining the abundance or diversity. They acknowledged identified an effect of habitat type (hedge versus field margin) rather than maturity *per se*, indicating that hedges provided the highest quality habitat, but that newly created field margins were nonetheless 'useful' in rapidly providing refuges for some taxa.

Just as Griffiths *et al*. (2007) have pointed to the contribution of degraded hedgerows to habitat heterogeneity in agro-ecosystems, I would emphasize the contribution even new hedgerows can make to invertebrate abundance and diversity. Equally, the presence, and therefore planting, of a hedgerow is clearly not optimal for all taxa.

In general, my results reflect the fact that maturation processes are subject to high degrees of 'interference' and disturbance in arable ecosystems, not only as a result of farming activities themselves, but also including management activity conducted as part of AES. In the case of farmland hedgerows, crop management activities in adjacent fields and hedgerow cutting frequency and extent can represent a disturbance despite the 'protection zone'. Regeneration techniques, such as laying and coppicing, will at least initially be highly disruptive to all kinds of organisms. Although hedgerows represent some degree of shelter and stability in rather unstable agro-ecosystems (Alford, 2011), they cannot remain immune from disturbance. The stability of ecological conditions that Thienemann saw as important to the development of diversity over time through the ageing process (McIntosh, 1985) is not guaranteed. Doing more to preserve this stability, *e.g.* by buffering hedgerows further, may help enhance invertebrate (and other) populations.

7.3. The influence of seasonality

Driessen *et al.* (2013) noted a lack of studies investigating seasonal responses of multi-order and multi-species invertebrate assemblages. Ideally, monitoring for invertebrate biodiversity should incorporate at year round view. Other hedgerow studies have focused on particular seasons. Joyce *et al*. (1997) and Pollard & Holland (2006) undertook sampling of broad invertebrate assemblages in summer, while Maudsley *et al.*

(2002) and Pywell *et al.* (2005) both looked at the effects of hedgerows on overwintering predatory arthropods in the tops and bottoms of hedgerows. Deeming *et al*. (2010) took a year round view of farmland hedgerows showing monthly variation in the invertebrate assemblages of the hedge bottom, which did not show an unequivocal link between summer and high abundance and diversity. In my study the effect of time or season (spring, summer, autumn) on invertebrate abundance and diversity was more apparent than any effect of hedgerow age.

Regarding the effect of month of sampling, patterns amongst taxa were variable, sometimes differing between boundary types, and this could be explained largely by descriptions of their ecologies and life cycles. Clearly there are divergent seasonal patterns in abundance: although for a majority of taxa summer was the peak month of abundance, a relatively large portion of the assemblage was more abundant in either spring or autumn. At both ground- and canopy level diversity indices showed relatively high diversity in September, comparable or even superior to July, which could well have been weather-dependent due to a wetter summer season and drier warm autumn. Analysis of both the broad assemblage and Coleoptera and Diptera families suggested that New hedges could offer certain characteristics that were favoured at different times of the year.

Sampling only in the summer, when insects are generally most abundant or at least most apparent, does not account for invertebrate taxa with different seasonal distributions. Biodiversity studies which focus only on summer surveys will miss significant components of invertebrate communities (Driessen *et al.*, 2013). Currently, some important long-term monitoring of invertebrate populations for environmental assessment of farmland takes place in summer only, *e.g.* by the Game and Wildlife Conservation Trust. Single season invertebrate surveying for biodiversity, potentially contribute to an underestimate of the importance of certain taxa within assemblages, and equally the importance of hedgerows as habitat at certain times of year. Increased monitoring of a range of taxa outside this peak season, including spring and autumn, such as that undertaken by the UK Butterfly Monitoring Scheme, would provide better understanding of the health of invertebrate populations, such as the impacts of climate change on farmland assemblages.

7.4. Other key factors affecting the invertebrate assemblage

Multivariate modelling suggested that although weather, at least in the short term, was the 'killer' factor in determining invertebrate abundance and diversity, shelter and protection supplied by a high sward and the density of foliage of the hedgerow itself seem to be important. The importance of hedgerows as shelter for invertebrate and other

wildlife is not new (*e.g.* Maudsley *et al*., 2000; Barr *et al.* 2005), yet the actual evidence for how shelter is provided and the way it might influence a range of invertebrate taxa is lacking.

It was perhaps surprising that measures of botanical diversity of the hedgerows were not more strongly correlated with invertebrate abundance or diversity, especially since Maudsley (2000) identified botanical diversity as a key factor in determining the diversity of hedgerow invertebrates. More recent research (Anderson *et al*., 2011) has indicated that low botanical diversity prevalent on conventionally managed arable farmland can be a poor predictor of arthropod diversity, but that vegetation structure (as measured by sward height) can have a relationship with parasitoid abundance and taxon (genera/family) richness, and with overall arthropod taxon richness. Some of the studies Maudsley (2000) reviewed stretch back over 30 years, and so it is perhaps conceivable that in the intervening period a significant decrease in botanical diversity of hedgerows has occurred. Hence, an effect of botanical diversity may now be now difficult to detect, although this would require more detailed analysis of botanical diversity at species level to verify. Maudsley (2000) was careful to point out that "not all associations between plant and invertebrate diversity are necessarily directly causal". Habitat structure and attributes associated with structural composition and diversity, such as sheltering qualities, seem to be important, rather than botanical taxonomic diversity *per se* (Kirby, 1993). I found that volume of hedge was less important for the assemblage than expected, although some taxa, *e.g.* Lepidoptera (dominated by moths), were associated with larger Mature hedges. Invertebrates are capable of exploiting even relatively small patches of suitable habitat (Kirby, 1993) and smaller New hedges have a part in contributing to structural diversity at a local and larger scale and in providing an element of shelter.

A widespread need at ground level for ample leaf litter and shelter from extremes of environmental conditions was identified from descriptions of the biologies of numerous taxonomic groups identified in this study. Maudsley, *et al.* (2002) also indicated the importance of hedge bottom vegetation biomass including leaf litter to a range of predatory arthropods. Leaf biomass/litter has not been measured directly in this study, although measures of hedgerow vegetation density (on ground and in canopy) and vegetation structure (sward height) were found to be important factors in determining abundance and diversity at ground level. Thinner canopies and sparser ground vegetation (allowing through increased light) was associated with a decrease in abundance and diversity in both the canopy and at ground level. An increase in sward height was associated with

increased diversity at ground level. Provision of favourable conditions in this respect was not found to be age-dependent and hedgerows of both types, relatively new plantings and Mature hedges, were seen to benefit the invertebrate assemblage as a whole.

Shelter is a function of the structure of both hedge top and bottom, which can be disrupted by management activities designed to enhance it. Reduced management of field boundaries can enhance the sheltering properties of a margin sward, at least in the short term. In a 2-year study, Blake *et al*. (2011) showed that a decrease of management intensity (including a zero cut regime), allowing field margin vegetation to grow in height and complexity, resulted in increased abundance and diversity of Auchenorrhyncha (Hemiptera). Griffiths *et al*. (2007) recommended that degraded hedgerows, which have had little or even no management, should be considered as a valuable part of habitat heterogeneity. Amy *et al.* (2015) found that unmanaged hedges supported higher abundances of predatory and herbivorous invertebrates than various restoration treatments. Given that loss of hedgerows through lack of management and resultant degradation is a primary concern of Hedgelink, this seems almost heretical to advocate non-intervention, but may make sense from the point of view of the value of 're-wilding' for conservation. In any case, its proponents are not advocating that management is abandoned completely for all hedgerows.

In this context, Hooper's work (1992, cited by Barr *et al.*, 2005) is interesting and relevant: he reported that for maximum value to invertebrates the best type of hedge was *unmanaged* and large, with an abundance of bramble (*Rubus fruticosus*). Given that current advice features more, not less, management of hedgerows under AES, this finding seems unlikely ever to be favoured by policy makers or farmers, especially since the latter regard the need to keep their land tidy a major factor in driving hedgerow management (Britt *et al*., 2011).

It is uncertain whether advice advocating a relaxation of management of field margins and hedgerows would be accepted, particularly if some of the main benefits might be to potential crop pests (see Blake *et al*., 2011). Since there is often a game and general ornithological interest amongst farmers, it should be easier to persuade them of the benefits of a 'hands-off' approach, if not for conservation of invertebrate populations, then as an important move to support the diet of farmland birds, including essential chick food (Wade *et al.*, 2008).

Weather will always be the most potent determinant of invertebrate abundance and diversity, and also of their apparency (Speight *et al*., 1999). It was a key determinant of

invertebrate diversity at ground level amongst the hedgerows/boundaries, although wind was a more important factor at canopy level. Invertebrates are heat and cold resistant to an extent, but any increase in the extremity and unpredictability of temperatures has the capacity to impact invertebrate populations negatively (Prather *et al*., 2013). A concurrent increase in unpredictable wind conditions is also likely to have a negative effect on the sheltering capacity of hedgerows. Increasing temperatures combined with wind and rain would tend to result in increased damage to hedgerows (Natural England and RSPB, 2014), and conditions which not all invertebrates may tolerate well over the longer term (Ewald *et al*., 2014).

Structural aspects of the hedgerow are able to provide some shelter from the elements. Higher swards or dense foliage can play a part in providing shelter from extremes of temperature, and so may have a small part to play in moderating climate change. Temperatures below a shady sward can be a few degrees lower than above the sward. Stewart *et al*. (2001) found that sward height had the effect of reducing temperatures at ground level, so that soil temperatures were lower the higher the sward. Nonetheless, to be sure that the true importance of sward height to invertebrates lies in its function in moderating temperature, and providing shelter from wind and rain, direct collection of microclimatic data would be necessary.

7.5. Utility of a higher taxon approach to measure invertebrate diversity

Wolton & Vergette (2012) aimed to record all species found within a single Devonshire farmland hedgerow, inventorying a range of wildlife taxa including all invertebrates. In view of the vast sizes of some groups, *e.g.* Diptera and Hymenoptera both consisting of ~7000 species (Barnard, 2011), full inventorying of invertebrates for biodiversity assessment would be impractical and costly on the scale required for monitoring. Besides the sheer size of some groups, there are other difficulties with identification of invertebrates down to species level, including the absence of up-to-date or complete keys for some groups (Barnard, 2011).

Bioindication, or surrogacy, employed as a short cut to biodiversity assessment, assumes the ability of one taxon to reflect the responses of a range of other taxa without testing directly (New, 1996). Research has shown, however, that surrogate schemes, although saving on time and costs, can be poor in protecting the total pool of taxa (Andelman & Fagan, 2000). There are dangers in trying to extrapolate the condition of invertebrate populations from limited taxa (Gruttke & Kornacker, 1995). The use of indicators is nonetheless widespread in assessments of diversity in agro-ecosystems.

There is little consensus for indicating biodiversity in agro-ecosystems: Araneae, Carabid and Staphylinid beetles, butterflies, Syrphids and other Diptera, Hymenoptera (Aculeata, Parasitica and Symphyta), Heteroptera etc – all have been proposed at one time or another as good correlates with overall species richness/biodiversity in farmland habitats (Duelli & Obrist, 1998, 1999, 2003; Billeter *et al*., 2008; Obrist & Duelli, 2010). Evaluations of non-crop semi-natural habitats, such as hedges and field margins, have often employed predatory arthropods, notably Araneae and/or Carabid beetles, as indicators or surrogates of habitat quality and invertebrate diversity (*e.g.* Petit & Burel, 1998; Holland *et al*., 2001; Maudsley *et al.*, 2002; Büchs, 2003b; Pywell *et al*., 2005; Fischer *et al*., 2013), although a greater range of other taxa, particularly functional groups, has been included in some studies (McAdam *et al.*, 1994; Joyce *et al*., 1997; Moreby & Southway, 2001; Pollard & Holland, 2006; Pywell *et al*., 2011; Amy *et al*., 2015).

Biaggini *et al.* (2007) suggested order level as a tool for assessing arthropod diversity in agro-ecosystems and in my study I extended this to include consideration of all broad taxonomic groups. I found inconclusive evidence for use of any single group as biodiversity indicators. Agri-environment schemes are typically implemented with little if any monitoring to show their effectiveness in supporting biodiversity (Anderson *et al*., 2011; Pywell *et al*., 2011). Lack of funding, manpower and expertise are bound to play a large part in this. A broad taxonomic approach using order level could be adopted more widely as a means of at least initial monitoring of invertebrate diversity (Biaggini *et al.*, 2007), thus providing a relatively cheap, basic conservation evaluation, by distinguishing between the effectiveness of different AES options. There may be a case for using this 'reductive' approach, given the evidence for depleted invertebrate diversity on farmland. Harrington *et al*. (2010), for instance, presented long-term data indicating declines in some insect taxa, and evidence of increased dominance by a few 'successful' abundant species in agro-ecosystems in the UK. Brooks *et al*. (2012) too indicated serious loss of insect biodiversity in the UK, including farmed land and semi-natural habitats.

There is a high likelihood that because of insufficient taxonomic knowledge, ecologists are not able to achieve an accurate picture of arable biodiversity (Nielsen & Nielsen, 2007). This is compounded by an acknowledged deficit and decline in identification skills with which organizations such as Invertebrate Link (JCCBI) are currently grappling. Greater use of a higher taxon approach for assessing invertebrate biodiversity in agro-ecosystems could be employed by relatively inexpert surveyors, as a stand-alone or a preliminary stage in more expert analysis (Biaggini *et al.*, 2007). The use

of ‘citizen scientists’, some of whom are relatively inexperienced, is an important consideration for UK conservation (Pocock *et al*., 2014), and the use of such an approach could enable greater participation in monitoring. The problem of enhancing taxonomic skills is a current issue, especially when it is alleged that “most graduates cannot use dichotomous keys” (Richard Chadd, Environment Agency, personal communication) and encouraging the increased use of keys, starting with recognition of broad taxonomic groups, would go some way towards promoting this discipline.

While not ideal in promoting deep taxonomic knowledge, a high-level (order/class) approach to invertebrate identification enables retention of broad biological information and could be capable of contributing to a broad understanding of distribution patterns of perhaps relatively understudied or under-represented taxa. It is also suitable in the absence of consensus, and indeed evidence, as to which, if any, taxon is most suitable as a surrogate for broader diversity. Caveats apply: resulting diversity values may appear low as a result of low taxonomic resolution, but this should not matter in the case of comparative studies.

Nonetheless, it seems unlikely that assessment of invertebrate diversity in agricultural environments will abandon use of certain well-known groups, such as beetles, spiders and butterflies, as indicators of invertebrate diversity. This is at least in part because knowledge and identification capabilities for these taxa are better and more widespread than for many other invertebrate taxa, but not because these groups are necessarily any better as surrogates for the diversity of other invertebrate taxa or indeed any more important as a component of biodiversity than other taxa. In the UK butterflies were until recently (pollinators were added in 2014) the only invertebrate group used as a national indicator for biodiversity, but account for only a small percentage of all species in agro-ecosystems (Büchs, 2003). Forty years of European research on Carabid beetles was recently celebrated (Kotze *et al*., 2011), and the use of Carabids as bioindicators for habitat assessment and conservation seems set to continue in farmed landscapes (*e.g*. Fischer *et al*., 2013). By contrast, important but relatively ‘difficult’ groups, such as parasitoid Hymenoptera are not generally used as tools for assessment in AES. In an effort to simplify matters, Anderson *et al*. (2011) proposed the use of the *abundance*, as opposed to species richness, of parasitoid Hymenoptera as a possible surrogate for invertebrate diversity (Araneae, Coleoptera, Diptera, Hemiptera), in assessing the fauna of agricultural grassland, and potentially for use in assessments of other habitats. My analyses showed that at ground level in the hedge bottoms only the abundance of Hymenoptera (containing many ants) was correlated with the abundance of the majority of other taxa in the

assemblage. At canopy level in the hedge tops I found a much weaker association of Hymenoptera and other single taxa. None was a perfect correlate for the invertebrate assemblage as a whole, although some were far better than others as candidates for 'substitution': in addition to Hymenoptera, Thysanoptera, Collembola, Hemiptera, Opiliones and Psocoptera all showed some relevance. Also, it was clear that there was no single taxon which was capable of discriminating between hedge types for all months/seasons. There was no completely satisfactory solution and this underlines once more the difficulty of taking a single taxon or indeed even a limited 'basket' of taxa to act as surrogates for invertebrate diversity overall. My study highlights the complexity of finding suitably effective surrogates for biodiversity evaluation, even when comparing fundamentally similar habitats and their components.

Billeter *et al*. (2008) made a pan-European (excluding the UK) study of biodiversity in agricultural landscapes, including hedgerow habitats, and were unable to identify a single group that could be used to predict the presence/biodiversity of other groups from a candidate list including vascular plants, birds, Araneae, Apoidea, Carabidae, Heteroptera and Syrphidae. The best surrogate for biodiversity was in fact a landscape parameter: an increase in semi-natural habitat was correlated with an increase in the species richness of all groups. Both Schmidt *et al.* (2005) and Fischer *et al*. (2013) have found that availability of living space, rather than habitat type, is a decisive factor in supporting spider diversity. Similarly, Holland *et al.* (2013) found that the proportion of uncropped land was positively related to butterfly diversity and bee density, as well as the abundance and diversity of plants and farmland birds. As indicated, my study found that some structural factors, presumably conferring larger living space, were important to invertebrate abundance and diversity. In addition, invertebrate taxon richness of the hedge bottom was greatest at the farm site with the greatest variety of landscape features (Riseholme), but this was not true for hedge canopy invertebrates.

7.6. Use of sampling methods

The sticky trapping technique has some potential for sampling from ground level, perhaps as a complement to pitfall trapping, since it seems particularly effective at sampling smaller organisms such as Acari and Collembola, parasitic wasps, small beetles such as Latridiidae and flies such as Phoridae and Sciaridae. The extent to which the dominance of such small organisms could be a reflection of diminution of body size amongst hedgerow invertebrates is uncertain and speculative: certainly a reduction in body size of organisms surviving mass extinction events, known as the Lilliput effect, has been

observed in the fossil record and many even be occurring in our oceans as a result of climate change (Garilli *et al*., 2015). There are certainly advantages to being small in depleted environments, since small organisms place much lower demands on their ecosystems. This may also have implications for food availability and quality for other wildlife, *e.g.* declining farmland bird species. A focal study using alternative sampling methods and morphometric/biomass analysis would provide more insight.

Beating in the canopy of hedgerows is capable of providing sufficient samples to enable biodiversity assessment (see also Amy *et al*., 2015), although use of a design incorporating a collection container (such as I have employed) is preferable to a conventional beating tray from which animals can more easily escape. There seemed to be far fewer invertebrates in the hedge canopy than perhaps expected, which I have attributed to the likely 'dynamism' of the canopy environment, but might also be ascribed to the 'short, sharp' beating protocol. There are some difficulties with regulating the force with which vegetation is jarred. In addition, further investigation of the effectiveness of different durations, frequencies and heights of beating for invertebrate surveying is desirable, since there is little standardisation to the extent seen for pitfall trapping for example (Drake *et al.*, 2007).

7.7. Use of diversity indices

In general, where a significant effect of hedge type was shown, this held true for all diversity indices, although there were some differences in coefficients and sometimes striking differences in their significance. In terms of the effects of the explanatory factors on diversity, again, in general there was a degree of uniformity in responses by the indices to the variables, albeit with a number of 'outliers'. Diversity indices, although essentially measuring the same thing, may not behave in the same way on the same dataset, and may even respond differently to the same set of variables. This is an important consideration for our understanding of how biodiversity responds to habitat destruction, creation and restoration in agro-ecosystems.

Given the way invertebrate assemblages in the hedgerows were dominated by a few highly abundant taxa, Berger-Parker as a dominance index has relevance. As Shannon *H*' is probably the most commonly used diversity index, its popularity is nonetheless likely to persist (Magurran, 2004). Technically there is no real reason to favour Shannon over other indices, but as with studying Carabids and use of pitfall trapping, familiarity and popularity are two highly important drivers in the use of any techniques. Recent work on hedgerow invertebrates by the CEH has used Shannon as the diversity index of choice (Amy *et al*.,

2015). Magurran (2004) advocates stronger justification in any biodiversity study relating to the choice of measure. As this study reinforces, these can affect perceptions of diversity and of the differences between habitats and assemblages, thereby affecting our understanding of the impacts of change.

7.8. The future of farmland hedgerows

Change has come to AES, and the key role of hedgerows is again evident. Basic farm payments will be dependent on 5% of a farm's land area being put into ecological protection, forming "Ecological Focus Areas" (Case, 2013; Driver, 2014); in terms of area, existing hedgerows will count towards that 5%. A fundamental need for living space is therefore recognised to an extent in these amendments.

Changes to Countryside Stewardship (Natural England, 2015) continue to provide for hedgerow management, but also renewed hedge planting. The emphasis is on "high quality hedgerows", which have various definitions relating not only to the presence of species of conservation concern, but also historic importance and contribution to local landscape character. Options make explicit reference to pollinators, but benefits for the invertebrate assemblage in general are presumably implied. Insects are otherwise seen as explicitly important only in terms of forage for farmland birds (Natural England, 2015). There is some sense that a concern for enhancing biodiversity *per se* is becoming overshadowed by more utilitarian considerations, notably 'ecosystem services' such as pollination (Stoate, 2014; Robertson, 2014). While the ecosystem services viewpoint is one that should effectively 'sell' the benefits of AES, researchers admit that there is still much that is not understood about 'service' provision by wildlife (Stoate, 2014) and warn that focusing too much on improvement of particular services may not necessarily benefit biodiversity (McKenzie, 2013). Indeed, AES options, such as hedge-planting and management, should do more than support crop pest control or pollination functions: they represent an attempt to protect and enhance diversity wholesale (Natural England, 2009), which will inevitably include taxa regarded in agriculture as (potentially) troublesome, or indeed without an obvious function. The role of agri-environmental hedgerow options in enhancing biodiversity is recognised, but plans for monitoring their achievements are not explicit. Using a range of taxa in a broader and shallower higher taxon approach may bring us closer to knowing what variety we have, if not how to value it.

It is right that hedges are prominent in greening requirements under Cross Compliance and also as voluntary measures under Stewardship, especially because we are still playing 'catch-up' in terms of restoring overall length of the hedgerow network.

Despite increased availability of AES funding for activities such as hedge planting and a general belief amongst farmers in the importance of hedgerows to wildlife, there are however still evident dangers to hedgerows, including an apparent underuse of conservation advice (Britt *et al*., 2011), but also less controllable factors such as climate.

7.9. Concluding comments on AES hedge planting and invertebrate assemblages

This study has shown that although relatively newly planted hedgerows may not support invertebrate assemblages as well as more mature hedges in some respects, they are nonetheless capable of contributing significantly to the abundance and biodiversity of farmland hedgerows within a short time-span (<15 years). Although mature habitats were more important to ground level invertebrate diversity, in the woody part of the hedgerow, older hedge habitats were not superior to much younger habitats as hypothesized. This might say less about the quality of the respectively-aged hedges than about the colonisation processes of invertebrates adapted to agro-ecosystems, their general ability to cope with 'ephemeral' conditions in the arable environment, and to rapidly exploit available non-crop habitat patches, irrespective of fragmentation. Also, it may be that this apparently rapid acquisition of characteristics of older habitats reflects low ambient levels of diversity in arable farmland and the varying levels and regularity of disturbance which can destabilize ecological communities (McIntosh, 1985). These factors could also help explain why, despite widespread insect diversity loss in the UK, hedgerow populations (of ground beetles) are reportedly "mostly stable" (Brooks *et al*., 2012).

New planting of hedgerows by farmers under revised Stewardship options (Natural England, 2015), should be a way of helping counteract the habitat simplification and degradation characteristic of agro-ecosystems (New, 2005a; Wade *et al.*, 2008; Natural England, 2012c). New planting can contribute to maintaining if not enhancing biodiversity by increasing fundamental space as well as heterogeneity/complementarity to established hedgerow habitats, and can represent a 'quick gain' to the invertebrate assemblage. Invertebrates are able to exploit relatively small habitat patches and many have no plant-specificity (Kirby, 1993), so that even relatively small improvements, such as young hedgerows, have the potential to make a difference to their abundance and diversity. Although hedgerows form an important component of non-crop habitats, they are not however a panacea for wildlife loss in the farmed landscape.

Greater emphasis on alternative or complementary options may be desirable for certain taxa, *e.g.* Lepidoptera. For instance, Fuentes-Montemayor *et al.* (2011a & b) regard a wider variety of landscape characteristics, such as increased woodland cover and

also scrub and grassland, as more beneficial to moth populations than hedgerows *per se*. My findings indicated that grassy hedgeless boundaries, with minimal management, offer different habitat conditions which support particular taxa well. Although not as taxon rich as hedgerows, they have qualities which can positively influence faunal communities by providing increased living space, refuges and dispersal corridors, adding to the heterogeneity of non-crop habitats available to ground-occurring invertebrates (Ernoult *et al*., 2013; Griffiths *et al.*, 2007).

While my study seems to suggest that hedgerow planting under AES is achieving its purpose in terms of extending and enhancing conditions for a broad range of invertebrate taxa within relatively short time-scales, further, and more detailed, taxonomic studies of canopy invertebrates would be required to establish whether this were true for taxa of conservation concern and how hedgerow planting contributes to invertebrate biodiversity in agro-ecosystems over the longer term. There is an obvious ongoing need to measure the success of our interventions and achievements through AES.

I do not fully agree with Robertson (2014) that farmland conservationists should not try to be 'deterministic' because 'Nature cannot be controlled', otherwise there would seem to be little point investing in agri-environmental schemes. Besides the need for sustainability and preservation of functionality, we have a moral and ethical responsibility to intervene, not necessarily to control Nature, but at least give a helping hand and make some reparation.

With this in mind, agri-environmental hedgerow planting can be seen to achieve the purpose of going some way towards replacing loss in the national stock and, combined with sympathetic stewardship can represent a relatively, perhaps surprisingly, quick gain by establishing habitats which provide essential extra living space and resources to support a broad spectrum of (perhaps modest) invertebrate diversity. For supporting different taxa throughout the seasons, a variety of habitats of different growth form and age are necessary. As such, it is the further intensification of land use, driven by climate change which has the capacity for greater impact on invertebrate populations over the longer term (Ewald *et al*., 2014). We can help to moderate any impacts on biodiversity by paying attention to restoration and enhancement of non-crop habitats of which hedgerows form a significant part.

References

ADAS (2004) *Hedgerow Management and Wildlife Review: further update, edit and publication* – BD2108. Available from: http://randd.defra.gov.uk/ [Accessed 22 Nov 2011]

Adis, J. (1979) Problems of interpreting arthropod sampling with pitfall traps. *Zoologischer Anzeiger Jena*, 202, 177-184

Agnarsson, I. (no date) *The Agnarsson Lab: Theridiidae – cobweb spiders* (Webpage). Available from: www.theridiidae.com/theridiidae.html [Accessed 28 March 2013]

Aikens, K. R. and Buddle, C. M. (2012) Small-scale heterogeneity in temperate forest canopy arthropods: stratification of spider and beetle assemblages. *Canadian Entomologist*, 144, 526-537

Aikens, K. R., Timms, L. L. and Buddle, C. M. (2013) Vertical heterogeneity in predation pressure in a temperate forest canopy. *PeerJ*, 1:e138, DOI 10.7717/peerj.138. Available from: https://peerj.com/articles/138/ [Accessed 20 Nov 2013]

Akaike, H. (1973) Information theory and an extension of the maximum likelihood principle. In : B. N. Petrov and F. Csaki (Eds.) *Second international symposium on information theory*, 267-281. Budapest: Academiai Kiado

Akaike, H. (1974) A new look at the statistical model identification. *IEEE Transactions on Automation Control*, 19, 716-723

Alexander, A., Butler, J. and Green, T. (2006) The value of different tree and shrub species to wildlife. *British Wildlife*, 18, 18-28

Alexander, K. N. A. (2011) *The Barkflies and Booklice (Psocoptera) of Cornwall and the Isles of Scilly*. Occasional Publications No. 3. Cornwall: CISFBR & ERCCIS

Alford, D. V. (1999) *A Textbook of Agricultural Entomology*. Oxford: Blackwell Science

Alford, D. V. (2011) *Plant pests*. London: Collins

Allen, R. E. (1990) *The concise Oxford dictionary of current English*. 8th edition. Oxford: Clarendon Press

Alvarez, T., Frampton, G. K. and Goulson, D. (2000) The role of hedgerows in the recolonisation of arable fields by epigeal Collembola. *Pedobiologia*, 44, 516-526

Amateur Entomologists' Society (no date) *A code of conduct for collecting insects and other invertebrates*: Invertebrate Link - Joint Committee for the Conservation of British Invertebrates [Internet]. Available from: http://www.amentsoc.org/ [Accessed 10 May 2013]

Amy, S. R., Heard, M. S., Harley, S. E., George, C. T., Pywell, R. F. and Staley, J. T. (2015) Hedgerow rejuvenation management affects invertebrate communities through changes to habitat structure. *Basic and Applied Biology*, 16, 443-451

Andelman, S. J. and Fagan, W. F. (2000) Umbrellas and flagships: Efficient conservation surrogates or expensive mistakes? *PNAS*, 97, 5954-5959

Andersen, A. (1997) Densities of overwintering carabids and staphylinids in cereal and grass fields and their boundaries. *Journal of Applied Entomology*, 121, 77-80

Andersen, A.N. (1999) My bioindicator or yours? Making the selection. *Journal of Insect Conservation*, 3, 61-64

Andersen, A. N., Hoffmann, B. D., Müller, W. J. and Griffiths, A. D. (2002) Using ants as bioindicators in land management: simplifying assessment of ant community responses. *Journal of Applied Ecology*, 39, 8-17

Anderson, A., McCormack, S. Helden, A., Sheridan, H., Kinsella, A. and Purvis, G. (2011) The potential of parasitoid Hymenoptera as bioindicators of arthropod diversity in agricultural grasslands. *Journal of Applied Ecology*, 48, 382-390

Andrewartha, H.G. and Birch L.C. (1954) *The Distribution and Abundance of Animals*. Chicago: The University of Chicago Press

Anteau, M. J. and Sherfy, M. H. (2010) Diurnal variation in invertebrate catch rates by sticky traps: Potential for biased indices of piping plover forage [Internet]. *Wetlands*, 30, 757-762. Available from: http://pubs.er.usgs.gov/publication/70037123 [Accessed 07 January 2015]

Asplund, J. and Wardle, D.A. (2012) Contrasting changes in palatability following senescence of the lichenized fungi *Lobaria pulmonaria* and *L. scrobiculata*. *Fungal Ecology*, 5, 710-713

Asteraki, E. J., Hart, B. J., Ings, T. C. and Manley, W. J. (2004) Factors influencing the plant and invertebrate diversity of arable field margins. *Agriculture, Ecosystems and Environment*, 102, 219-231

Ausden, M. and Drake, M. (2006) Invertebrates. In: W. Sutherland (Ed.) *Ecological Census Techniques: a handbook*. Second Edition, 214-249. Cambridge: Cambridge University Press

Baini, F., Pitzalis, M., Taiti, S., Vigna Taglianti, A., Zapparoli, M. and Bologna, M. A. (2012) Effects of reforestation with Quercus species on selected arthropod assemblages (Isopoda Oniscidea, Chilopoda, Coleoptera: Carabidae) in a Mediterranean area. *Forest Ecology and Management*, 286, 183-191

Balmford, A., Green, M. J. B. and Murray, M. G. (1996) Using higher-taxon richness as a surrogate for species richness: I. Regional tests. *Proceedings of the Royal Society of London B*, 263, 1267-1274

Barnard, P. C. (2011) *The Royal Entomological Society Book of British Insects*. Chichester: Wiley-Blackwell

Barnes, G. and Williamson, T. (2006) *Hedgerow History: Ecology, History and Landscape Character*. Oxford: Windgather Press

Barr, C. and Petit, S. (Eds.) (2001) *Hedgerows of the World: their ecological functions in different landscapes*. Proceedings of the tenth annual IALE (UK) conference. IALE (UK)

Barr, C. J., Britt, C. P. and Sparks, T. H. (Eds.) (1995) *Hedgerow Management and Wildlife*. Institute of Terrestrial Ecology/ADAS report to the Ministry of Agriculture, Fisheries and Food

Barr, C. J., Britt, C. P., Sparks, T. H. and Churchward, J. M. (2005) *Hedgerow Management and Wildlife: a review of research on the effects of hedgerow management and adjacent land on biodiversity*. London: Defra

Bates, F. S. and Harris, S. (2009) Does hedgerow management on organic farms benefit small mammal populations? *Agriculture, Ecosystems & Environment*, 129, 124-130

Bealey, C., Ledder, E., Robertson, H. and Wolton, R. (2009) Hedgerows – their wildlife, current state and management needs. *British Wildlife*, 20, 323-329

Bell, J. R., Gates, S., Haughton, A. J., Macdonald, D. W., Smith, H., Wheater, C. P. and Cullen, W. R. (1999) Pseudoscorpions in field margins: effects of margin age, management and boundary habitats. *The Journal of Arachnology*, 27, 236-240

Bell, S. S., McCoy, E. D. and Mushinsky, H. R. (1991) *Habitat Structure: the physical arrangement of objects in space*. London: Chapman and Hall

Benjamini, Y. and Hochberg, Y. (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society B*, 57, 289-300

Benjamini, Y. and Yekutieli, D. (2001) The control of the false discovery rate in multiple testing under dependency. *Annals of Statistics*, 29, 1165-1188

Bennett, A. F. (2003). *Linkages in the Landscape: The Role of Corridors and Connectivity in Wildlife Conservation*. Gland, Switzerland and Cambridge: IUCN

Bennett, S. L., Eady, P. E. and Deeming, D C. (2013) Invertebrate biodiversity within the grassy and woody elements of farmland hedgerows. In: N. Boatman, M. Green, J. Marshall, K. Musters, W. Peach, S. Peel, G. Siriwardena and B. Smith (Eds.) *Aspects of Applied Biology 118, Environmental Management on Farmland*, 253-258. Warwick: AAB

Benton, T. G., Bryant, D. M., Cole, M., Crick, H. Q. P. (2002) Linking agricultural practice to insect and bird populations: an historical study over three decades. *Journal of Applied Ecology*, 39, 673-687

Benton, T. G., Vickery, J. A. and Wilson, J. D. (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology and Evolution*, 18, 182-188

Berger, W. H. and Parker, F. L. (1970) Diversity of planktonic Foraminifera in deep sea sediments. *Science*, 168, 1345-1347

Besnard, A. G. and Secondi, J. (2014) Hedgerows diminish the value of meadows for grassland birds: Potential conflicts for agri-environment schemes. *Agriculture, Ecosystems and Environment*, 189, 21-27

Betbeder, J., Nabucet, J., Pottier, E., Baudry, J., Corgne, S. and Hubert-Moy, L. (2014) Detection and characterization of hedgerows using TerraSAR-X imagery. *Remote Sensing*, 6, 3752-3769

Betts, C., Laffoley, D. D'A., and Cribb, P. W. (1986) *The Hymenopterist's Handbook*. The Amateur Entomologist, Volume Seven (Second Edition). Hanworth: The Amateur Entomologists' Society

Biaggini, M., Consorti, R., Dapporto, L., Dellacasa, M., Paggetti, E. and Corti, C. (2007) The taxonomic level order as a possible tool for rapid assessment of Arthropod diversity in agricultural landscapes. *Agriculture, Ecosystems & Environment*, 122, 183-191

Billeter, R., Liira, J., Bailey, D., Bugter, R., Arens, P., Augenstein, I., Aviron, S., Baudry, J., Bukacek, R., Burel, F., Cerny, M., De Blust, G., De Cock, R., Diekötter, T., Dietz, H., Dirksen, J., Dormann, C., Durka, W., Frenzel, M., Hamersky, R., Hendrickx, F., Herzog, F., Klotz, S., Koolstra, B., Lausch, A., Le Coeur, D., Maelfait, J. P., Opdam, P., Roubalova, M., Schermann, A., Schermann, N., Schmidt, T., Schweiger, O., Smulders, M. J. M., Speelmans, M., Simova, P., Verboom, J., van Wingerden, W. K. R. E, Zobel, M. and Edwards, P. J. (2008) Indicators for biodiversity in agricultural landscapes: a pan-European study. *Journal of Applied Ecology*, 45**,** 141-150

Bird, S., Coulson, R. N., Crossley Jr., D. A. (2000) Impacts of silvicultural practices on soil and litter arthropod diversity in a Texas pine plantation. *Forest Ecology and Management*, 131, 65-80

Black, R. (2011) Last December UK's coldest for 100 years [Internet]. *BBC News, Science & Environment*, 5 January. Available from: http://www.bbc.co.uk [Accessed 10 January 2015]

Blackburn, J., Farrow, M. and Arthur, W. (2002) Factors influencing the distribution, abundance and diversity of geophilomorph and lithobiomorph centipedes. *Journal of Zoology*, 256, 221-232

Blake, R. J., Woodcock, B. A., Ramsay, A. J., Pilgrim, E. S., Brown, V. K., Tallowind, J. R. and Potts, S. G. (2011) Novel margin management to enhance Auchenorrhyncha biodiversity in intensive grasslands. *Agriculture, Ecosystems and Environment*, 140, 506-513

Boatman, N. D., Blake, K. A., Aebischer, N. J. and Sotherton, N. W. (1994) Factors affecting the herbaceous flora of hedgerows on arable farms and its value as wildlife habitat. In: T. A. Watt and G. P. Buckley (Eds.) *Hedgerow Management and Nature Conservation*, 33-46. Ashford: Wye College Press

Boatman, N., Green, M., Holland, J., Marshall, J., Renwick, A., Siriwardena, G., Smith, B. and de Snoo, G. (2010a) *Aspects of Applied Biology 100, Agri-environment schemes – What have they achieved and where do we go from here?* Warwick: Association of Applied Biologists

Boatman, N., Jones, N., Gaskell, P. and Dwyer, J. (2010b) Monitoring of agri-environment schemes in the UK. In: N. Boatman, M. Green, J. Holland, J. Marshall, A. Renwick, G. Siriwardena, B. Smith, and G. de Snoo. (Eds.) *Aspects of Applied Biology 100, Agri-environment schemes – What have they achieved and where do we go from here?*, 9-18. Warwick: Association of Applied Biologists

Boatman, N., Ramwell, C., Parry, H., Jones, N., Bishop, N. J., Gaskell, P., Short, C., Mills, J. and Dwyer, J. (2008) *A review of environmental benefits supplied by agri-environment schemes*. Peterborough: LUPG. Available from: www.lupg.org.uk [Accessed 22 November 2011] *This organisational website no longer exists.

Bolker, B. M., Brookes, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H. and White, J-S. S. (2008) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution*, 24, 127-135

Bouget, C., Larrieu, L. and Brin, A. (2014) Key features for saproxylic beetle diversity derived from rapid habitat assessment in temperate forests. *Ecological Indicators*, 36, 656-664

Bouget, C. and Duelli, P. (2004) The effects of windthrow on forest insect communities: a literature review. *Biological Conservation*,118, 281-299

Boutin, C., Martin, P. A. and Baril, A. (2009) Effects of plant diversity and landscape features on arthropods in organic and conventional farming systems. *Ecoscience*, 16, 492-501

Boutin, C., Baril, A., McCabe, S. K., Martin, P. A. and Guy, M. (2011) The value of woody hedgerows for moth diversity on organic and conventional farms. *Environmental Entomology*, 40, 560-569

Bozdogan, H. (1987) Model selection and Akaike's Information Criterion (AIC): the general theory and its analytical extensions. *Psychometrika*, 52, 345-370

BRC [Biological Records Centre] (no date) National Barkfly Recording Scheme (Britain and Ireland): Introduction to Barkflies. Available from: www.brc.ac.uk [Accessed 20 October 2013]

Bristowe, W. S. (1949) The Distribution of Harvestmen (Phalangida) in Great Britain and Ireland, with Notes on their Names, Enemies and Food. *Journal of Animal Ecology*, 18,100-114

Britt, C., Barr, C., Sparks, T. (2005) Overall conclusions on the effects of management on wildlife and priorities for further research. In: C. J. Barr, C. P. Britt, T. H. Sparks and J. M. Churchward (Eds.) *Hedgerow Management and Wildlife: A Review of Research on the Effects of Hedgerow Management and Adjacent Land on Biodiversity*, 82-94. London: Defra

Britt, C., Tuffnell, N., Kirkham, F., Roberts, A. and Sparks, T. (2011) *Hedgerow Management: A Survey of Land Managers' and Contractors' Practices and Attitudes*. Defra Project BD2117 [Internet]. Available from: www.hedgelink.org.uk [Accessed 29 January 2013]

Brooks, D. R., Bater, J. E., Clark, S. J., Monteith, D. T., Andrews, C., Corbett, S. J. , Beaumont, D. A., Chapman, J. W. (2012) Large carabid beetle declines in a United Kingdom monitoring network increases evidence for a widespread loss in insect biodiversity. *Journal of Applied Ecology*, 49, 1009-1019

BTO/RSPB (2014) *Observatory monitoring framework – indicator fact sheet. Environmental impact: Biodiversity, Indicator DE5: Farmland bird populations* [Internet]. Available from: https://www.gov.uk/ [Accessed 20 November 2015]

Büchs, W. (2003a) Sampling, Trapping and Rearing of Pedators. In: D. V. Alford (Ed.) *Biocontrol of Oilseed Rape Pests*, 235-244. Oxford: Blackwell Science

Büchs, W. (2003b) Biodiversity and agri-environmental indicators – general scopes and skills with special reference to the habitat level. *Agriculture, Ecosystems & Environment*, 98, 35-78

Buddle, C. (2013) Arthropod Ecology. Canopy: Lunch in the tree-tops for the birds and bugs [Internet]. Available from: http://arthropodecology.com/2013/09/19/lunch-in-the-tree-tops-for-the-birds-and-the-bugs/ [McGill University blog] [Accessed 2 November 2013]

Buglife (no date) *Managing farmland habitats for invertebrates: Hedgerows and Cereal Field Margins* [Internet]. Available from: www.buglife.org.uk [Accessed 25 October 2013]

Bultman, T. L. and Uetz, G. W. (1982) Abundance and community structure of forest floor spiders following litter manipulation. *Oecologia*, 55, 34-41

Burel, F. (1992) Effect of landscape structure and dynamics on species diversity in hedgerow networks. *Landscape Ecology*, 6, 161 - 174

Burel, F. (1998) Landscape structure effects on carabid beetle spatial patterns in western France. Landscape Ecology, 2, 215–226

Burel, F. and Baudry, J. (1994) Control of biodiversity in hedgerow network landscapes in western France. In: T. A. Watt and G. P. Buckley (Eds.) *Hedgerow Management and Nature Conservation, British Ecological Society Conservation Ecology Group, Wye College, University of London, 4-5 September 1992*, 47-57. Ashford: Wye College Press

Burel, F. and Baudry, J. (2012) Hedgerow connectivity. In: J. Dover (Ed.) *Hedgerow Futures*: Proceedings of the first international Hedgelink Conference held at Staffordshire University, Stoke-on-Trent, UK, 3 - 5 September, 75-86. Leeds: Natural England

Burel, F., Butet, A., Delettre, Y. R., Millan de la Pena, N. (2004) Differential response of selected taxa to landscape context and agricultural intensification. *Landscape and Urban Planning*, 67, 195-204

Butler, S. J., Vickery, J. A. and Norris, K. (2007) Farmland Biodiversity and the Footprint of Agriculture. *Science*, 315, 381-384

Butterfly Conservation (2013) *2012: A Disaster Year for UK Butterflies* [Internet]. Available from: www.butterfly-conservation.org. [Accessed 18 April 2013]

Cameron, R. A. D. (1970) The effect of temperature on the activity of three species of Helicid snail (Mollusca: Gastropoda). *Journal of Zoology*, 162, 303-315

Cameron, R. A. D. (1984) The biology and history of hedges: exploring connections. *Biologist*, 31, 203-208

Cameron, R. (2003) *Keys for the identification of Land Snails in the British Isles*. Shrewsbury: Field Studies Council

Capinera, J. L. (2010) *Featured Creatures: European earwig, Forficula auricularia Linnaeus (Insecta: Dermaptera: Forficulidae)* [Internet]. Available from: http://entnemdept.ufl.edu [Accessed 10 December 2014]

Carey, P. D., Wallis, S., Chamberlain, P. M., Cooper, A., Emmett, B. A., Maskell, L. C., McCann, T., Murphy, J., Norton, L. R., Reynolds, B., Scott, W. A., Simpson, I. C., Smart, S. M. and Ullyett, J. M. (2008) *Countryside Survey: UK Results from 2007*. NERC/Centre for Ecology & Hydrology, (CEH Project Number: C03259). Available from: http://www.countrysidesurvey.org.uk/ [Accessed 22 November 2011]

Carroll, M. J. (2012) The Ecology Of British Upland Peatlands: Climate Change, Drainage, Keystone Insects And Breeding Birds. PhD thesis, University of York

Carroll, M. J., Dennis, P., Pearce-Higgins, J. W. and Thomas, C. D. (2011) Maintaining northern peatland ecosystems in a changing climate: effects of soil moisture, drainage and drain blocking on craneflies**.** *Global Change Biology*, 17**,** 2991-3001

Carter, D. J. (1984) *Pest Lepidoptera of Europe with Special Reference to the British Isles*. Dordrecht: Dr W. Junk/Kluwer Academic

Case, P. (2013) Greening: How different farms will be affected [Internet]. *Farmers Weekly*, 31 October. Available from: http://www.fwi.co.uk/ [Accessed 25 April 2014]

Cavanaugh, J. E. (2012) 171:290 Model Selection. Lecture III: Corrected AIC and modified AIC, AICc and MAIC. University of Iowa [Internet]. Available from: http:myweb.uiowa.edu/cavaaugh/ms_lec_3_ho.pdf [Accessed 3 February 2014]

Chalmers, N. and Parker, P. (1989) *The OU project guide: Fieldwork and statistics for ecological projects*. Preston Montford: Field Studies Council

Chandler, P. (Ed.) (2010) *A dipterist's handbook*. London: Amateur Entomologists' Society.

Chao, A., Jost, L., Chiang, S.C., Jiang, Y.-H. & Chazdon, R.L. (2008) A two-stage probabilistic approach to multiple community similarity indices. *Biometrics*, 64, 1178-1186

Chapman, J. W., Reynolds, D. R., Smith, A. D., Riley, J. R., Telfer, M. G. and Woiwod, I. P. (2005) Mass aerial migration in the carabid beetle *Notiophilus biguttatus. Ecological Entomology*, 30, 264-272

Chapman, L. (2001) The Living History of Our Hedgerows: A Guide to Dating Hedgerows. Chudleigh: Orchard Publications

Chen, S. S. (2010) Quantifying Landscape Connectivity: A GIS-based Approach. *World Academy of Science, Engineering and Technology*, 46, 30-37

Chinery, M. (2007) *Domino Guide to the Insects of Britain and Western Europe*. London: A&C Black

Chown, S. L. and McGeoch, M. A. (2011) Chapter 18: Measuring biodiversity in managed landscapes. In: A. Magurran, and B. J. McGill (Eds.) *Biological Diversity: Frontiers in Measurement and Assessment*. Oxford: Oxford University, 252-264

Clements, D. K. and Tofts, R. J. (1992) Hedgerow Evaluation and Grading System (HEGS): a methodology for the ecological survey, evaluation and grading of hedgerows. Test Draft. Countryside Planning and Management

Clements, D. K. & Tofts, R. J. (1992) Hedges make the grade. A look at the wildlife value of hedges. *British Wildlife*, 4, 87-95

Clifford, H. T. and Stephenson, W. (1975) *An introduction to numerical classification*. London: Academic Press

Coleman, D. C., Crossley Jr., D. A., Hendrix, P. F. (2004) *Fundamentals of Soil Ecology*. Burlington: Elsevier Academic Press

Collins, K. L., Boatman, N. D., Wilcox, A. and Holland, J. M. (2003) A 5-year comparison of overwintering polyphagous predator densities within a beetle bank and two conventional hedgebanks. *Annals of Applied Biology*, 143, 63-71

Corbet, G. B. and Collis, G. (2010) *Scottish Invertebrate Species Knowledge Dossier. Isopoda (Non-marine Woodlice & Waterlice).* Available from: www.buglife.org.uk [Accessed 10 January 2014]

Corbett, S. and Mole, A. (2005) *Invertebrates and Hedgerows. In: C. J. Barr, C. P. Britt, T. H. Sparks, and J. M. Churchward (Eds.) Hedgerow Management and Wildlife. A review of research on the effects of hedgerow management and adjacent land on biodiversity*, 35-46. London: Defra

Cornwallis, R. K. (1969) Farming and wildlife conservation in England and Wales. *Biological Conservation*, 1, 142-147

Critchley, C. N. R., Fowbert, J. A., Sherwood, A. J. and Pywell, R. F. (2006) Vegetation development of sown grass margins in arable fields under a countrywide agri-environment scheme. *Biological Conservation*, 132, 1-11

De Cauwer, B., Reheul, D., De Laethauwer, S., Nijs, I. and Milbau, A. (2006) Effect of light and botanical species richness on insect diversity. *Agronomy for Sustainable Development*, 26, 35-43

Davidson, M. B. (2012) Scottish Invertebrate Species Knowledge Dossier: Opiliones (Harvestmen) [Internet]. Available from: http://www.buglife.org.uk [Accessed 10 January 2014]

Davies, E. (2014) *Farmland butterflies bounce back.* 19th February [Internet]. Available from: www.bbc.co.uk/nature [Accessed 20 November 2015]

Davies, Z. G. and Pullin, A. S. (2007) Are hedgerows effective corridors between fragments of woodland habitat? An evidence-based approach. *Landscape Ecology*, 22, 333-351

Davis, B. N. K. (1991) *Insects on nettles*. Naturalists' Handbooks 1. Slough: Richmond Publishing Co. Ltd.

Davis, M. (2014) A Dendrologist's Handbook. Chesham: The Dendrologist

Deckers, B., Hermy, M. and Muys, B. (2004) Factors affecting plant species composition of hedgerows: relative importance and hierarchy. *Acta Oecologica*, 26, 23–37

Deeming, D. C., Bennett, S. L. and Morrant, C. (2010) Effect of hedge maturity on composition of invertebrate assemblages at a site in Lincolnshire. In: N. Boatman, M. Green, J. Holland, J. Marshall, A. Renwick, G. Siriwardena, B. Smith and G. de Snoo (Eds.) *Aspects of Applied biology 100, Agri-environment schemes – What have they achieved and where do we go from here?*, 397-403

Defra (2007) *Hedgerow Survey Handbook*. *A standard procedure for local surveys in the UK*. London: Defra

Defra (2011a) *Biodiversity 2020: A strategy for England's wildlife and ecosystem services* [Internet]. London: Department for Available from: https://www.gov.uk/government/ [Accessed 08 Sept 2015]

Defra (2011b) *UK Biodiversity Indicators in your pocket 2011*. London: Defra. Available from: http://jncc.defra.gov.uk/pdf/BIYP_2011.pdf [Accessed 19 October 2011]

Defra (2012) Observatory monitoring framework - indicator data sheet. Environmental impact: Biodiversity. DE6: Population trends for farmland butterflies [Internet]. Available from: www.naturalengland.org.uk [Accessed 15 April 2013]

Defra (2013a) *Biodiversity 2020: a strategy for England's wildlife and ecosystem services. Indicators 2013* [Internet]. London: Defra. Available from: www.gov.uk/defra [Accessed 23 October 2013]

Defra (2013b) *Science and Research Projects: Understanding the biodiversity benefits of the component parts of the hedgerow - BD5214* [Internet]. Available from: www.http://randd.defra.gov.uk/, Homepage > Science and Research Projects > Science Search > Science and Research Projects [Accessed 20 November 2013]

Defra (2014) *Common Agricultural Policy Schemes in England: August 2014 update*. Available from: www.gov.uk/cap-reform [Accessed 10 September 2015]

Defra (2015) *Agriculture in the United Kingdom 2014* [Internet]. Available from: www.gov.uk/government/statistics [Accessed 15 September 2015]

Defra/JNCC (2013) *UK Biodiversity Indicators in Your Pocket 2013* [Internet]. Available from: www.jncc.defra.gov.uk/biyp [Accessed 10 January 2014]

Defra/JNCC (2014) *UK Biodiversity Indicators 2014* [Internet]. Available from: www.jncc.defra.gov.uk/ukbi [Accessed 10 September 2015]

Defra/RPA (2012) *The Guide to Cross Compliance in England* [Internet]. Sheffield: Rural Payments Agency. Available from: http://rpa.defra.gov.uk [Accessed 10 January 2013]

Dennis, P. (1997) Impact of forest and woodland structure on insect abundance and diversity. In: A. D. Watt, N. E. Stork and M. D. Hunter (Eds.) *Forests and Insects*, 321-340. London: Chapman & Hall

Dennis, P., Young, M. R. and Bentley, C. (2001) The effects of varied grazing management on epigeal spiders, harvestmen and pseudoscorpions of *Nardus stricta* grassland in upland Scotland. *Agriculture, Ecosystems and Environment*, 86, 39–57

Dickinson, T. (2003) *Wild Flowers: an easy guide by habitat and colour*. Totnes: Green Books Ltd

Didham, R. K. (1997) An overview of invertebrate responses to forest fragmentation. In: A. D. Watt, N. E. Stork and M. D. Hunter (Eds.) *Forests and Insects*, 303-320. London: Chapman & Hall

Diehl, E., Mader, V. L., Wolters, V., and Birkhofer, K. (2013) Management intensity and vegetation complexity affect web-building spiders and their prey. *Oecologia*, 173, 579-589

Disney, R. H. L., Erzinclioglu, Y. Z., de C. Henshaw, D. J, Howse, D., Unwin, D. M, Withers, P., and Woods, A. (1982) Collecting methods and the adequacy of attempted fauna surveys with reference to the Diptera. *Field Studies*, 5, 607-621

Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B. and Collen, B. (2014) Defaunation in the Anthropocene. *Science*, 345, 401-406

Docherty, M. and Leather, S. R. (1997) Structure and abundance of arachnid communities in Scots and lodgepole pine plantations. *Forest Ecology*, 95, 197-207

Dornelas, M., Soykan, C. and Ugland, K. I. (2011) Chapter 17: Biodiversity and disturbance. In: A. Magurran, and B. J. McGill (Eds.) (2011) *Biological Diversity: Frontiers in Measurement and Assessment*. Oxford: Oxford University, 237-251

Dover, J. W. (Ed.) (2012) *Hedgerow Futures*: Proceedings of the first International Hedgelink Conference held at Staffordshire University, Stoke-on-Trent, UK, 3-5 September. London: The Tree Council/Hedgelink

Dover, J. (1996) Factors affecting the distribution of satyrid butterflies on arable farmland. *Journal of Applied Ecology*, 33, 723-734

Dover, J. W., Sparks, T. H. and Greatorex-Davies, J. N. (1997) The importance of shelter for butterflies in open landscapes. *Journal of Insect Conservation*, 1, 89-97

Dover, J. and Sparks, T. (2000) A review of the ecology of butterflies in British hedgerows. *Journal of Environmental Management*, 60, 51-63

Dowdeswell, W. H. (1987) *Hedgerows and Verge.* London: Allen & Unwin

Drake, C. M., Lott, D. A., Alexander, K. N. A. and Webb, J. (2007) *Surveying terrestrial and freshwater invertebrates for conservation evaluation*. Natural England Research Report NERR005. Sheffield: Natural England

Driessen, M. M., Kirkpatrick, J. B. and McQuillan, P. B. (2013) Shifts in composition of monthly invertebrate assemblages in Moorland differed between lowland and montane locations but not fire-ages. *Environmental Entomology*, 42, 58-73

Driver, A. (2014) *How England's new agri-environment scheme will work*, 6 March 2014 [Internet]. Source: www.farmersguardian.com [Accessed 15 April 2014]

Duelli, P. (1997) Biodiversity evaluation in agricultural landscapes: an approach at two different scales. *Agriculture, Ecosystems and Environment*, 62, 81-91

Duelli, P. and Obrist, M. K. (1998) In search of the best correlates for local organismal biodiversity in cultivated areas. *Biodiversity & Conservation*, 7, 297-309

Duelli, P. and Obrist, M. K. (2003) Biodiversity indicators: the choice of values and measures. *Agriculture, Ecosystems and Environment*, 98, 87-98

Duelli, P., Obrist, M. K., and Schmatz, D. R. (1999) Biodiversity evaluation in agricultural landscapes: above-ground insects. *Agriculture, Ecosystems and Environment*, 74, 33-64

Dunkley, F.A. & Boatman, N.D. (1994). Preliminary findings from a study of sown and unsown management options for the restoration of perennial hedge-bottom vegetation. In: N. D. Boatman (Ed.) *Field Margins: Integrating Agriculture and Conservation*, 329-334. BCPC Monograph No 58. Farnham: British Crop Protection Council

Dytham, C. (2011) *Choosing and using statistics: a biologist's guide* (3rd edition). Oxford: Wiley-Blackwell

Dziock, F. and Sarthou, J-P. (2005) *A review of the use of hoverflies as bioindicators (Diptera, Syrphidae).* Presentation given at the 3rd Syrphidae Symposium, Leiden, The Netherlands, 2nd to 5th September 2005 [Internet]. Available from: http://syrphidae.com/docs/Dziock_Sarthou_bioindication_review.pdf. [Accessed 3 April 2013]

Ecoscope (2003) *Review of Agri-Environment Scheme: Monitoring Information and Research and Development Results*. Report to Defra. St Ives: Ecoscope Applied Ecologists.

Ernoult, A., Vialatte, A., Butet, A., Michel, N., Rantier, Y., Jambon, O., and Burel, F. (2013) Grassy strips in their landscape context, their role as new habitat for biodiversity. *Agriculture, Ecosystems and Environment*, 166, 15-27

Ewald, J., Wheatley, C. J., Aebischer, N. J., Duffield, S., Morecroft, M. and Crick, H. P. Q. (2014) *Cereal invertebrates, extreme events and long-term trends in climate: Final Report*. [Internet]. Available from: www.naturalengland.org.uk [Accessed 17 January 2016]

Eyre, M. D., Luff, M. L. and Leifert, C. (2013) Crop, field boundary, productivity and disturbance influences on ground beetles (Coleoptera, Carabidae) in the agroecosystem. *Agriculture, Ecosystems & Environment*, 165, 60-67

Facey, S. L., Botham, M. S., Heard, M. S., Pywell, R. F. and Staley, J. T. (2014) Moth communities and agri-environment schemes: Examining the effects of hedgerow cutting regime on diversity, abundance, and parasitism. *Insect Conservation and Diversity*, 7, 543-552

Faith, D. P. (2008) Biodiversity. In: The Stanford Encyclopedia of Philosophy, E. N. Zalta (Ed.) [Internet]. Available from: http://plato.stanford.edu/archives/fall2008/entries/biodiversity/ [Accessed 21 September 2015]

Farrow, R. (2011) The effect of hedgerow age on the biodiversity of winged insects on arable farmland in Lincolnshire. Unpublished undergraduate dissertation at the University of Lincoln

FCMCD (2006) Franklin County Mosquito Control District: *Insects Commonly Mistaken for Mosquitoes* [Internet]. Available from: http://www.fcmcd.org/mistaken.html [Accessed 8 August 2013]

Field, A. (2009) *Discovering statistics using SPSS* (3rd edition). London: Sage Publications Ltd.

Field, G. N., Gardiner, T., Mason, C. F. and Hill, J. (2007) Agri-environment schemes and butterflies: the utilization of two metre arable field margins. *Biodiversity and Conservation*, 16, 465-475

Fischer, C., Schlinkert, H., Ludwig, M., Holzschuh, A., Galle, R., Tscharntke, T. and Batary, P. (2013) The impact of hedge-forest connectivity and microhabitat conditions on spider and carabid beetle assemblages in agricultural landscapes. *Journal of Insect Conservation*, 17, 1027-1038

Fitter, R., Fitter, A. and Blamey, M. (1985) *The wild flowers of Britain and Northern Europe*. London: William Collins Sons and Co Ltd.

Flohre, A., Fischer, C., Aavik, T., Bengtsson, K., Berendse, F., Bommarco, R., Ceryngier, P., Clement, L. W., Dennis, C., Eggers, S., Emmerson, M., Geiger, F., Guerrero, I., Hawro, V., Inchausti, P., Liira, J., Morales, M. B., Osate, J. J., Paert, T., Weisser, W. W., Winqvist, C., Thies, C. and Tscharntke, T. (2011) Agricultural intensification and biodiversity partitioning in European landscapes comparing plants, carabids and birds. *Ecological Applications*, 21, 1772-1781

Floren, A. (2008) Abundance and ordinal composition of arboreal arthropod communities of various trees in old primary and managed forests. In: A. Floren and J. Schmidl (Eds.) (2008) *Canopy arthropod research in Europe: Basic and applied studies from the high frontier,* 279-298. Nürnberg: Bioform

Floren, A. and Schmidl, J. (Eds.) (2008) *Canopy arthropod research in Europe: Basic and applied studies from the high frontier*. Nürnberg: Bioform

Foelix, R. F. (1996) *Biology of Spiders*. London: Oxford University Press.

Forman, R. T. T. and Baudry, J. (1984) Hedgerows and hedgerow networks in landscape ecology. *Environmental Management*, 8, 495-510

Fournier, E. and Loreau, M. (1999) Effects of newly planted hedges on ground beetle diversity (Coleoptera, Carabidae) in an agricultural landscape. *Ecography*, 22, 87-97

Fowler, J., Cohen, L. and Jarvis, P. (1998) *Practical Statistics for Field Biology* (2nd edition). Chichester: John Wiley & Sons

Fox, R., Brereton, T.M., Asher, J., Botham, M.S., Middlebrook, I., Roy, D.B. and Warren, M.S. (2011) *The State of the UK's Butterflies 2011*. Wareham, Dorset: Butterfly Conservation and the Centre for Ecology & Hydrology

Frampton, G. K., Gould, P. J., van den Brink, P. J. and Hendy, E. (2007) Type 'A' and 'B' recovery revisited: the role of field-edge habitats for Collembola and macroarthropod community recovery after insecticide treatment. *Environmental Pollution*, 145, 874-883

Freeman, P. (1983) *Handbooks for the Identification of British Insects: Sciarid Flies (Diptera, Sciaridae)*. London: Royal Entomological Society

Fry, R. and Lonsdale, D. (Eds.) (1991) *Habitat Conservation for Insects - a neglected green issue*. The Amateur Entomologist, Volume 21. Hanworth: The Amateur Entomologists' Society

Fuentes-Montemayor, E., Goulson, D. and Park, K. J. (2011a) Pipistrelle bats and their prey do not benefit from four widely applied agri-environment management prescriptions. *Biological Conservation*, 144, 2233-2246

Fuentes-Montemayor, E., Goulson, D., and Park, K. J. (2011b) The effectiveness of agri-environment schemes for the conservation of farmland moths: assessing the importance of a landscape scale management approach. *Journal of Applied Ecology*, 48, 532-542

Fuller, R. J. and Warren, M. S. (1993) *Coppiced woodlands: their management for wildlife*. Peterborough: JNCC

GWCT - Game and Wildlife Conservation Trust (no date a) *Do beetles eat spiders?* [Internet]. Available from: http://www.gwct.org.uk/ [Accessed 20 June 2013]

GWCT - Game and Wildlife Conservation Trust (no date b) *Changes in cereal invertebrates* [Internet]. Available from: http://www.gwct.org.uk/ [Accessed 10 October 2013]

Game and Wildlife Conservation Trust (2013) *Chick-food insects and pesticides in Sussex and Loddington*. Available from: http://www.gwct.org.uk/ [Accessed 01 December 2013]

Garbutt, R. A. and Sparks, T. H. (2002) Changes in the botanical diversity of a species-rich ancient hedgerow between two surveys (1971-1998). *Biological Conservation*, 106, 273-278

Gardiner, M. M., Landis, D. A., Gratton, C., Schmidt, N., O'Neal, M., Mueller, E., Chacon, J., Heimpel, G. E. and DiFonzo, C. D. (2009) Landscape composition influences patterns of native and exotic lady beetle abundance. *Diversity and Distributions*, 15, 554-564

Garilli, V., Rodolfo-Metalpa, R., Scuderi, D., Brusca, L., Parrinello, D., Rastrick, S. P. S., Foggo, A., Twitchett, R. J., Hall-Spencer, J. M. and Milazzo, M. (2015) Physiological advantages of dwarfing in surviving extinctions in high-CO_2 oceans. *Nature Climate Change*, 5, 678-682

Gaston, K. J. (1994) *Rarity*. London: Chapman & Hall

Gaston, K. J. (2000) Biodiversity: higher taxon richness. *Progress in Physical Geography*, 2000, 24, 117

Gaston, K. J. and Williams, P. H. (1993) Mapping the world's species – the higher taxon approach. *Biodiversity Letters*, 1, 2-8

Gerlach, J., Samways, M. and Pryke, J. (2013) Terrestrial invertebrates as bioindicators: an overview of available taxonomic groups. *Journal of Insect Conservation*, 17, 831-850

Gibb, T. J. and Oseto, C. Y. (2006) *Arthropod Collection and Identification: Field and Laboratory Tecniques*. Burlington, San Diego, London: Academic Press

Gibbons, B. (1995) *Field Guide to Insects of Britain and Northern Europe*. Marlborough: The Crowood Press

Gimaret-Charpentier, C., Pelissier, R., Pascal, J. P. and Houllier, F. (1998) Sampling strategies for the assessment of tree species diversity. *Journal of Vegetation Science*, 9, 161-172

Godfrey, A. (2003) *A review of the invertebrate interest of coarse woody debris in England*. English Nature Research Reports: Number 513. Peterborough: English Nature

Goeden, R. D. and Louda, S. M. (1976) *American Review of Entomology*, 21, 325-342

Golovatch, S. I and Kime, R. D. (2009) Millipede (Diplopoda) distributions: A review. *Soil Organisms*, 81, 565–597

Gotelli, N. J. and Ellison, A. M. (2004) *A Primer of Ecological Statistics*. Sunderland, MA: Sinauer Associates, Inc.

Gottschalk, T. K., Dittrich, R., Diekötter, T., Sheridan, P., Wolters, V. and Ekschmitt (2010) Modelling land-use sustainability using farmland birds as indicators. *Ecological Indicators*, 10, 15-23

Goulson, D. (2010) Bumblebees. In: N. Maclean (Ed.) *Silent Summer: The State of Wildlife in Britain and Ireland*, 415 - 429. Cambridge: Cambridge University Press.

Grafen, A. and Hails, R. (2002) *Modern Statistics for the Life Sciences*. Oxford: Oxford University Press

Green, B. H. (1975) The future of the British countryside. *Landscape and Planning*, 2, 179-195

Greenslade, P. J. M. (1973) Sampling ants with pitfall traps: digging-in effects. *Insectes Sociaux*, 20, 343-353

Grice, P. V., Radley, G. P., Smallshire, D. and Green, M. R. (2007) Conserving England's arable biodiversity through agri-environment schemes and other environmental policies: a brief history. *Aspects of Applied Biology*, 81, 7-22

Griffiths, G. J. K., Winder, L., Holland, J. M., George Thomas, C. F. and Williams, E. (2007) The representation and functional composition of carabid and staphylinid beetles in different field boundary types at a farm scale. *Biological Conservation*, 135, 145-152

Gruppe, A., GoBner, M., Engel, K. and Simon, U. (2008) Vertical and horizontal distribution of arthropods in temperate forests. In: A. Floren and J. Schmidl (Eds.) (2008) *Canopy arthropod research in Europe: Basic and applied studies from the high frontier*, 383-405. Nürnberg: Bioform

Gruttke, H. (1994) Dispersal of carabid species along a linear sequence of young hedge plantations. In: K. Desender (Ed.) *Carabid beetles: ecology and evolution*, 299-303. The Netherlands: Kluwer Academic Publishers

Gruttke, H. and Kornacker, P. M. (1995) The development of epigeic fauna in new hedges - a comparison of spatial and temporal trends. *Landscape and Urban Planning*, 31, 217-231

Gruttke, H. and Willecke, S. (1993) Tieroekologische Langzeitstudie zur Besiedlung neu angelegter Gehoelzpflanzungen in der intensiv bewirtschafteten Agrarlandschaft – ein E+E-Vorhaben. [The colonization of newly planted hedge-like woodlots in an intensely cultivated landscape, a zooecological long-term investigation – a project supported by the German government]. *Natur und Landschaft*, 68, 367-376

Gullan, P. J. and Cranston, P. S. (2005) *The Insects: An Outline of Entomology*. Oxford: Blackwell Publishing

Hallett, R. H., Goodfellow, S. A. and Heal, J. D. (2007) Monitoring and detection of the swede midge (Diptera: Cecidomyiidae). *The Canadian Entomologist*, 139, 700-712

Hammer, O. (no date) Past: Multivariate Statistics [Internet]. Available from: http://folk.uio.no/ohammer/past [Accessed 01 Oct 2012]

Hanley M. E. and Wilkins J. P. (2015) On the verge? Preferential use of road-facing hedgerow margins by bumblebees in agro-ecosystems. *Journal of Insect Conservation*, 19, 67-74

Hansard (1987) H.C. Vol. 121, col. 713 (4 November) [Internet]. Available from: http://hansard.millbanksystems.com/ [Accessed 21 October 2013]
Hansard (1995a) H.C. Vol. 258, col. 59 (18 April) [Internet]. Available from: http://hansard.millbanksystems.com/ [Accessed 21 October 2013]
Hansard (1995b) H. L. Vol. 561, col. 401 (9 February) [Internet]. Available from: http://hansard.millbanksystems.com/ [Accessed 21 October 2013]
Hanski, I. and Gyllenberg, N. (1997) Uniting two general patterns in the distribution of species. *Science*, 275, 397-400
Harde, K. W. and Severa, F. (2009) *Der Kosmos Käferführer* [The Kosmos Beetle Guide]. Stuttgart: Kosmos
Harrington, R., Shortall, C. R. and Woiwod, I. P. (2010) Aerial insect biomass: trends from long-term monitoring. In: N. Maclean (Ed.) *Silent Summer: The State of Wildlife in Britain and Ireland*, 540 – 555. Cambridge: Cambridge University Press
Hatley, C. L. and MacMahon, J. A. (1980) Spider community organization: seasonal variation and the role of vegetation architecture. *Environmental Entomology*, 9, 632-639
Hawkins, D. (2009) *Biomeasurement*. Oxford: Oxford University Press
Hayes, M. J., Jones, A. T., Sackville Hamilton, N. R., Wildig, J. and Buse, A. (2001) Studies on the restoration of Welsh hedges. In: C. Barr and S. Petit (Eds.) *Hedgerows of the World: their ecological functions in different landscapes*, 339-348. UK: IALE
Hedgelink (2009) *The importance of hedgerows and the services they provide to society. Key messages* [Internet]. Available from: www.hedgelink.org.uk [Accessed 10 January 2010]
Hedgelink (2014) *Farm Environment Schemes* [Internet]. Available from: www.hedgelink.org.uk [Accessed 28 January 2014]
Hedgelink (no date a) *Wildlife and hedgerows* [Internet]. Available from: www.hedgelink.org.uk [Accessed 20 October 2013]
Hedgelink (no date b) *UK hedgerow legislation* [Internet]. Available from: www.hedgelink.org.uk [Accessed 20 October 2013]
Hedgelink (no date c) *Hedgerow Biodiversity Action Plan* [Internet]. Available from: www.hedgelink.org.uk [Accessed 15 November 2013]
Hedgelink (no date d) *Importance of hedges and hedgerows* [Internet]. Available from: www.hedgelink.org.uk [Accessed 30 January 2014]
Hedgelink (no date e) *Hedgerow management* [Internet]. Available from: www.hedgelink.org.uk [Accessed 18 April 2014]
Hedgelink (no date f) *The Hedge Management Cycle* [Internet]. Available from: http://www.hedgelink.org.uk/assets/docs/Hedgelink%20A5%2012pp%20leaflet_7.pdf [Accessed 18 April 2014]
Hegarty, C.A., McAdam, J.H. & Cooper, A. (1994) Factors influencing the plant species composition of hedges: Implications for management in Environmentally Sensitive Areas. In N. Boatman (Ed.), *Field Margins: Integrating Agriculture and Conservation*. *BCPC Monograph No*. 58, 227-234. Farnham: British Crop Protection Council
Heino, J. and Soininen, J. (2007) Are higher taxa adequate surrogates for species-level assemblage patterns and species richness in stream organisms? *Biological Conservation*, 137, 78-89
Heip, C. (1974) A new index measuring evenness. *Journal of the Marine Biological Association of the UK*, 54, 555-557
Heip, C. and Engels, P. (1974) Comparing species diversity and evenness indices. *Journal of the Marine Biological Association of the UK*, 54, 559-563
Herzog, F. (2005) Agri-environment schemes as landscape experiments. *Agriculture, Ecosystems & Environment*, 108, 175-177
Henriques, S., Pais, M. P., Batista, M. I., Costa, M. J. and Nogueira Cabral, H. (2013) Response of fish-based metrics to anthropogenic pressures in temperate rocky reefs. *Ecological Indicators*, 25, 65-76
Hill, D., Fasham, M., Tucker, G., Shewry, M. and Shaw, P. (Eds.) (2005) *Handbook of Biodiversity Methods: Survey, Evaluation and Monitoring*. Cambridge: Cambridge University Press
Hillyard, P. D. (2005) *Harvestmen (Opiliones)*. Synopses of the British Fauna 4. Preston Montford: Field Studies Council

Hinsley, S. A. and Bellamy, P. E. (2000) The influence of hedge structure, management and landscape context on the value of hedgerows to birds: A review. *Journal of Environmental Management*, 60, 33-49

Hof, A. R. and Bright, P. W. (2010) The value of agri-environment schemes for macro-invertebrate feeders: hedgehogs on arable farms in Britain. *Animal Conservation*, 13, 467-473

Hof, A. R., Snellenberg, J., and Bright, P. W. (2012) Food or fear? Predation risk mediates edge refuging in an insectivorous mammal. *Animal Behaviour*, 83, 1099-1106

Hodge, I. and Reader, M. (2010) The introduction of Entry Level Stewardship in England: extension or dilution in agri-environment policy? *Land Use Policy*, 270-282

Hoffmann, S. and Hoffmann, A. (2008) Is there a "true" diversity? *Ecological Economics*, 65, 213-215

Holland, J. M. (2002) Carabid beetles, their ecology, survival and use in agroecosystems. In: J. M. Holland (Ed.) *The Agroecology of Carabid Beetles*, 1-40. Andover: Intercept

Holland, J.M., Begbie, M., Birkett, T., Reynolds, C.J.M and Thomas, C.F.G. (2001). The influence of hedgerows on coleopteran distributions: results from a multifield sampling study. In C. Barr & S. Petit (Eds.) *Hedgerows of the World: their ecological functions in different landscapes*, 177-186. IALE (UK)

Holland, J. M. and Fahrig, L. (2001) Landscape woody border increases insect diversity in alfalfa fields. In: C. Barr and S. Petit (Eds.) *Proceedings of the 2001 Annual IALE (UK) conference, held at Birmingham University, 5th – 8th September. Hedgerows of the World: Their Ecological functions in Different Landscapes,* 167-176. IALE (UK)

Holland, J. M. and Luff, M. L. (2000) The effects of agricultural practices on Carabidae in temperate agro-ecosystems. *Integrated Pest Management Reviews*, 5, 109-129

Holland, J. M., Oaten, H., Moreby, S., Birkett, T., Simper, J., Southway, S. and Smith, B. M. (2012) Agri-environment scheme enhancing ecosystem services: A demonstration of improved biological control in cereal crops. *Agriculture, Ecosystems & Environment*, 155, 147-152

Holland, J. M., Oaten, H., Southway, S. and Moreby, S. (2008) The effectiveness of field margin enhancement for cereal aphid control by different natural enemy guilds. *Biological Control*, 47, 71-76

Holland, J.M., Storkey, J., Lutman, P. J. W., Henderson, I. and Orson, J. (2013) The Farm4Bio project: managing uncropped land for biodiversity. *Aspects of Applied Biology*, 118, 89-99

Hollier, J. A. (2008) The Barklice (psocoptera) associated with an old-field succession in southern Britain. *British Journal of Entomological Natural History*, 21, 143-147

Holt, E. A. and Miller, S. W. (2010) Bioindicators: Using Organisms to Measure Environmental Impacts. *Nature Education Knowledge*, 3, 8. Available from: http://www.nature.com/scitable [Accessed 10 November 2014]

Hooker, C. A. (1992) Responsibility, ethics and nature. In: D. E. Cooper & J. A. Palmer (Eds.) *The Environment in Question*, 147-164. London: Routledge

Hooper, M. (1992) *Hedge Management*. Unpublished: Institute of Terrestrial Ecology report for the Department of the Environment.

Hooper, M. (2004) *The History of Hooper's Hedgerow Hypothesis* [Internet]. Available from: http://www.bna-naturalists.org/mags/aut-wintr04/hedges.html [Accessed 22 November 2011]

Hooper, M. D. and Holdgate, M. W. (1968) *Hedges and hedgerow trees*. Proceedings of Monks Wood Symposium No. 4, 25th – 26th November. Norwich: Nature Conservancy

Hopkin, S. P. (1991) *A Key to the Woodlice of Britain and Ireland*. Shrewsbury: FSC

Hopkin, S. P. (1997) *Biology of the Springtails (Insecta: Collembola)*. Oxford: OUP

Hopkin, S. P. (2002) Collembola. In : R. Lal (Ed.) *Encyclopaedia of Soil Science,* 207-210. New York: Marcel Dekker

Hopkin, S. P. (2007) *A Key to the Collembola (Springtails) of Britain and Ireland*. Shrewsbury: FSC

Hsieh, Y.-L. and Linsenmair, K. E. (2012) Seasonal dynamics of arboreal spider diversity in a temperate forest. *Ecology and Evolution*, 2, 768-777

IACR (2000) *Guidelines for hedge management to improve the conservation value of different types of hedge* – Final Project Report – BD2102. Available from: http://randd.defra.gov.uk/default.aspx [Accessed 10 November 2013]

IBM Corp. (2010) IBM SPSS Statistics for Windows, Version 19.0. Armonk, NY: IBM Corp

IBM (no date) Can SPSS do a nonparametric or rank analysis of covariance (Quade's test)? [Internet – IBM Support Portal]. Available from: https://www-304.ibm.com/support/docview.wss?uid=swg21477497 [Accessed 11 November 2012]

IGER (2000) *Welsh ESA Field margins and Hedges*. London: MAFF

JNCC (no date) *UK BAP list of priority habitats* [Internet]. Available from: http://jncc.defra.gov.uk [Accessed 23 October 2013]

Jakovlev, J. (2011) Fungus gnats (Diptera: Sciaroidea) associated with dead wood and wood growing fungi: new rearing data from Finland and Russian Karelia and general analysis of known larval microhabitats in Europe. *Entomologica Fennica*, 22, 157-189

Jaremovic, R. and Rollo, C. D. (1979) Tree climbing by the snail *Cepaea nemoralis* (L) – possible method for regulating temperature and hydration. *Canadian Journal of Zoology*, 57, 1010-1014

Jennings, S. B., Brown, N. D. and Sheil, D. (1999) Assessing forest canopies and understorey illumination: canopy closure, canopy cover and other measures. *Forestry*, 72, 59-73

Jones-Walters, L. M. (1989) Keys to the families of British spiders. *Field Studies*, 9, 365-443

Jones, F. G. W. and Jones, M. G. (1984) *Pests of Field Crops*. *Third Edition*. London: Edward Arnold

Jost, L. (no date) *Critical Review of Anne Magurran's Measuring Biological Diversity* [Internet]. Available from: http://www.loujost.com/ [Accessed 25 January 2011]

Jost, L., DeVries, P., Walla, T., Greeney, H., Chao, A. and Ricotta, C. (2010) Partitioning diversity for conservation analyses. *Diversity and Distributions*, 16, 65-76

Joyce, K. A., Jepson, P. C., Doncaster, C. P. and Holland, J. M. (1997) Arthropod distribution patterns and dispersal processes within the hedgerow. In: A. Cooper and J. Power (Eds.) *Species Dispersal and Land Use Processes*. *Proceedings of the sixth annual IALE (UK) conference, held at the University of Ulster, 9th – 11th September 1997*, 103-110

Kardol, P., Newton, J. S., Bezemer, T. M., Maraun, M., van der Putten, W. H. (2009) Contrasting diversity patterns of soil mites and nematodes in secondary succession. *Acta Oecologica*, 35, 603-609

Kass, G.V. (1980) An exploratory technique for investigating large quantities of categorical data. *Applied Statistics*, 29, 119-127

Kennedy, C. E. J. and Southwood, T. R. E. (1984) The Number of Species of Insects Associated with British Trees: A Re-Analysis. *Journal of Animal Ecology*, 53, 455-478

Kervinen, M., Alatalo, R. V., Lebigre, C., Siitari, H. and Soulsbury, C. D. (2012) Determinants of yearling male lekking effort and mating success in black grouse (*Tetrao tetrix*). *Behavioural Ecology*, 23, 1209-1217

Keylock, C. J. (2005) Simpson diversity and the Shannon–Wiener index as special cases of a generalized entropy. *Oikos*, 109, 203-207

Kirby, P. (1993) *Habitat management for invertebrates: a practical handbook*. Sandy: RSPB

Kirk, W. D. J. (1992) *Insects on cabbages and oilseed rape.* Naturalists' Handbooks 18. Slough: Richmond Publishing Co. Ltd

Kleijn, D., Rundlöf, M., Scheper, J. Smith, H. G. and Tscharntke, T. (2011) Does conservation on farmland contribute to halting the biodiversity decline? *Trends in Ecology and Evolution*, 26, 474-481

Klein, D. and Sutherland, W. J. (2003) How effective are European agri-environment schemes on conserving and promoting biodiversity. *Journal of Applied Ecology*, 40, 947-970

Kotzageorgis, G. C. and Mason, C. F. (1997) Small mammal populations in relation to hedgerow structure in an arable landscape. *Journal of the Zoological Society of London*, 242, 425-434

Kotze, D. J., Brandmayr, P., Casale, A., Dauffy-Richard, E., Dekoninck, W., Koivula, M. J., Lövei, G. L., Mossakowski, D., Noordijk, J., Paarmann, W., Pizzolotto, R., Saska, P., Schwerk, A., Serrano, J., Szyszko, J., Taboada, A., Turin, H.,Venn, S., Vermeulen, R. and Zetto, T. (2011) Forty years of carabid beetle research in Europe – from taxonomy, biology, ecology and population studies to bioindication, habitat assessment and conservation [Internet]. *ZooKeys*, 100, 55-148. Available from: www.zookeys.org [Accessed 30 April 2014]

Krebs, C. J. (1999) *Ecological methodology*, 2nd edition. New York: Harper & Row

Kremen, C. (2005) Managing ecosystem services: what do we need to know about their ecology? *Ecology Letters*, 8, 468-479

Krewenka, K. M., Holzschuh, A., Tscharntke, T. and Dormann, C. T. (2011) Landscape elements as potential barriers and corridors for bees, wasps and parasitoids. *Biological Conservation*, 144, 1816-1825

Kromp, B. (1999) Carabid beetles in sustainable agriculture: a review on pest control efficacy, cultivation impacts and enhancement. *Agriculture, Ecosystems & Environment*, 74, 187-228

Kromp, B. and Hartl, W. (1991) Untersuchung ökologischer Wechselbeziehungen zwischen agrarlandschaftlichen Strukturelementen und Ackerflächen [Investigation of ecological interactions between structural elements of agricultural landscapes and arable farmland], Vienna, Unpublished Research Report

Landcare Research (2010) *Identification and surveillance: Sticky traps* [Internet]. Available from: http://www.landcareresearch.co.nz/research/biocons/invertebrates/idsurveillance [Accessed 4 April 2010]

Lange, M., Gossner, M. M. and Weisser, W.W. (2011) Effect of pitfall trap type and diameter on vertebrate by-catches and ground beetle (Coleoptera: Carabidae) and spider (Araneae) sampling. *Methods in Ecology and Evolution*, 2, 185-190.

Larrivée, M. and Buddle, C. M. (2009) Diversity of canopy and understorey spiders in north-temperate hardwood forests. AGRICULTURAL AND FOREST ENTOMOLOGY, *11, 225-237*

Laurance, W. F. (2007) Have we overstated the tropical biodiversity crisis? *Trends in Ecology and Evolution*, 22, 65-70

Lawson, A. (1983) Rank Analysis of Covariance: Alternative Approaches. *Journal of the Royal Statistical Society. Series D (The Statistician)*, 32, 331-337

Lawton, J. H. and Schroder, D. (1977) Effects of plant type, size of geographical range and taxonomic isolation on number of insect species associated with British plants. *Nature*, 265, 137-140

Lawton, J. H., Bignell, D. E., Bolton, B., Bloemers, G. F., Eggleton, P., Hammond, P. M., Hodda, M., Holt, R. D., Larsen, T. B., Mawdesley, N. A., Stork, N. E., Srivastava, D. S. and Watt, A. D. (1998) Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature*, 391, 72-76

Lazzaro, L., Otto, S. and Zanin, G. (2008) Role of hedgerows in intercepting spray drift: evaluation and modeling of effects. *Agriculture, Ecosystems and Environment*, 123, 317-327

Le Viol, I., Julliard, R., Kerbiriou, C., de Redon, L., Carnino, N., Machon, N. And Porcher, E. (2008) Plant and spider communities benefit differently from the presence of planted hedgerows in highway verges. *Biological Conservation*, 141, 1581-1590

Lechner, M. (1991) Untersuchung der epigaeischen Makrofauna fuenfjaehriger Feldhecken [Investigation of the epigeic macrofauna of 5-year-old hedges]. *Veroeffentlichungen Naturschutz Landschaftspflege Baden-Wuerttemberg*, 66, 415-466

Ledder, E. (no date) Agri-environment Schemes – what has been achieved and what changes are planned? [Internet]. Available from: www.hedgelink.org.uk [Accessed 20 October 2012]

Lee, B. (1985) *British Naturalists' Association Guide to Fields, Farms and Hedgerows*. Marlborough: The Crowood Press

Lee, M. S. Y. (1997) Documenting present and past biodiversity: conservation biology meets palaeontology. *Trends in Ecology and Evolution*, 12, 132-33

Legendre, P. and Legendre, L. (2012) *Numerical Ecology*. Third English Edition. Amsterdam: Elsevier B.V.

Lewis, T. (1969a) The distribution of flying insects near a low hedgerow. *Journal of Applied Ecology*, 6, 443-452

Lewis, T. (1969b) The diversity of the insect fauna in a hedgerow and neighbouring fields. *Journal of Applied Ecology*, 6, 453-458

Linsenmaier, K. E., Davis, A. J., Fiala, B. and Speight, M. R. (2001) Tropical Forest Canopies: Ecology and Management. Dordrecht: Kluwer Academic Publishers

Lipsitz, L. A. and Goldberger, A. L. (1992) Loss of 'Complexity' and Aging: Potential Applications of Fractals and Chaos Theory to Senescence. *JAMA*, 267, 1806-1809

Longino, J. T. , Coddington, J. and Colwell, R. K. (2002) The ant fauna of a tropical rain forest: estimating species richness three different ways. *Ecology*, 83, 689-702

Luff, M. L. (2007) *The Carabidae (ground beetles) of Britain and Ireland*. *Handbooks for the Indentification of British Insects, Volume 4 Part 2 (Second edition).* St Albans: Royal Entomological Society

MacArthur, R. H. and Wilson. E. O. (1967) *The Theory of Island Biogeography*. Princeton: Princeton University Press

Mace, G. (2012) BES President's piece on science feeding policy. *The Bulletin of the British Ecological Society*, June, 43, 3

McAdam, J. H., Bell, A. C. and Henry, T. (1994) The effect of restoration techniques on hedge flora and microfauna. In: T. A. Watt and G. P. Buckley (Eds.) *Hedgerow Management and Nature Conservation, British Ecological Society Conservation Ecology Group, Wye College, University of London, 4-5 September 1992*, 25-32. Ashford: Wye College Press

McCollin, D. (Ed.) (2000) Hedgerows: perspectives on biodiversity and environmental management. Selected papers from the 'Hedgerow Conservation: policy, protection and evaluation' meeting, University College Northampton, July 21 1999. *Journal of Environmental Management*, 60

McCollin, D. (2000) Editorial. Hedgerow policy and protection - changing paradigms and the conservation ethic. *Journal of Environmental Management*, 60, 3-6

McDonald, B. (2007) Effects of Vegetation Structure on Foliage Dwelling Spider Assemblages in Native and Non-native Oklahoma Grassland Habitats. *Proceedings of the Oklahoma Academy of Science*, 87, 85-88

McGavin, G. C. (2001) *Essential Entomology. An Order-by-Order Introduction*. Oxford: OUP

McGill, B. J., Etienne, R. S., Gray, J. S., Alonso, D., Anderson, M. J., Benecha, H. K., Dornelas, M., Enquist, B. J., Green, J. L., He, F., Hurlbert, A. H., Magurran, A., Marquet, P. A., Maurer, B. A., Ostling, A., Soykan, C. U., Ugland, K. I. and White, E. P. (2007) Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecology Letters*, 10, 995-1015

McIntosh, R. P. (1985) *The Background of Ecology: Concept and Theory*. Cambridge: Cambridge University Press

McIntyre, S., Barrett, G. W., Kitching, R. L. and Recher, H. F. (1992) Species triage: seeing beyond wounded rhinos. *Conservation Biology*, 6, 604-606

McKenzie, A. J., Emery, S. B., Franks, J. R. and Whittingham, M. J. (2013) Landscape-scale conservation: collaborative agri-environment schemes could benefit both biodiversity and ecosystem services, but will farmers be willing to participate? *Journal of Applied Ecology*, 50, 1274-1280

Macfadyen, S., Craze, P. G., Polaszek, A., van Achterberg, K. and Memmott, J. (2011) Parasitoid diversity reduces the variability in pest control services across time on farms. *Proceedings of the Royal Society B – Biological Sciences*, 278, 3387-3394

Maclean, M. (2006) *Hedges and hedgelaying: a guide to planting, management and conservation*. Marlborough: The Crowood Press

Maclean, M. (2003) *Resource Management: Hedges*. Marlborough: The Crowood Press

Maclean, M. (1992) *New Hedges for the Countryside*. Ipswich: Farming Press Books

Maclean, N. (Ed.) (2010) *Silent Summer: The State of wildlife in Britain and Ireland*. Cambridge: Cambridge University Press

MacLeod, A., Wratten, S. D., Sotherton, N. W. and Thomas, M. B. (2004) 'Beetle banks' as refuges for beneficial arthropods in farmland. Long-term changes in predator communities and habitat. *Agriculture and Forest Entomology*, 6, 147-154

Magurran, A. (2004) *Measuring Biological Diversity*. Oxford: Blackwell Publishing

Magurran, A. and McGill, B. J. (Eds.) (2011) *Biological Diversity: Frontiers in Measurement and Assessment*. Oxford: Oxford University

Mallis, R. E. and Rieske, L. K. (2011) Arboreal spiders in eastern hemlock. *Environmental Entomology*, 40, 1378-1387

Margalef, R. (1972) Homage to Evelyn Hutchinson, or why is there an upper limit to diversity? *Transactions of the Connecticut Academy of Arts and Sciences*, 33, 211-235

Marshall, E. J. P., West, T. M. and Maudsley, M. J. (2001) Treatments to restore the diversity of herbaceous flora of hedgerows. In: C. Barr and S. Petit (Eds.) *Proceedings of the 2001 Annual IALE (UK) conference, Hedgerows of the World: Their Ecological functions in Different Landscapes*, 319-328. UK: IALE

Marshall, S. A., Anderson, R. S., Roughley, R. E., Behan-Pelletier, V. and Danks, H. V. (1994) *Terrestrial Arthropod Biodiversity: Planning a Study and Recommended Sampling Techniques: A Brief Prepared by the Biological Survey of Canada (Terrestrial Arthropods)*[Internet]. Ottawa: Biological Survey of Canada [Accessed 20 March 2010]

Martin, M, Bastardie, F., Richard, D. and Burel, F. (2001) Studying boundary effects on animal movement in heterogeneous landscapes: the case of *Abax ater* (Coleoptera: Carabidae) in hedgerow network landscapes. *Sciences de la vie / Life Sciences*, 324, 1029-1035

Maudsley, M. J. (2000) A review of the ecology and conservation of hedgerow invertebrates in Britain. *Journal of Environmental Management*, 60, 65-76

Maudsley, M., West, T., Rowcliffe, H. and Marshall, E. J. P. (1997) Spatial variability in plant and insect (Heteroptera) communities in hedgerows in Great Britain. In: A. Cooper and J. Power (Eds.) *Species Dispersal and Land Use Processes. Proceedings of the Sixth Annual Conference of the International Association of Landscape Ecologists*, 229-236.

Maudsley, M., Seeley, B. and Lewis, O. (2002) Spatial distribution patterns of predatory arthropods within an English hedgerow in early winter in relation to habitat variables. *Agriculture, Ecosystems and Environment*, 89, 77-89

Meek, B., Loxton, D., Sparks, T., Pywell, R., Pickett, H. and Nowakowskic, M. (2002) The effect of arable field margin composition on invertebrate biodiversity. *Biological Conservation*, 106, 259-271

Mensink, P. J. and Henry, H. A. L. (2011) Rain events influence short-term feeding preferences in the snail *Cepaea nemoralis*. *Journal of Molluscan Studies*, 77, 241-247

Mercer, C., Cherrill, A., Tudor, G. & Andrews, M. (1999) Hedgerow plant communities: relationships with adjacent land use and aspect. *Aspects of Applied Biology*, 54, 345-352

Merckx, T. and van Dyck, H. (2007) Habitat fragmentation affects habitat-finding ability of the speckled wood butterfly, *Pararge aegeria* L. *Animal Behaviour*, 74, 1029-1037

Merckx, T., Feber, R. E., Riordan, P., Townsend, M. C., Bourn, N. A. D., Parsons, M. S., Macdonald, D. W. (2009) Optimizing the biodiversity gain from agri-environment schemes. *Agriculture, Ecosystems & Environment*, 130, 177-182

Merckx, T., Marini, L., Feber, R. E. and Macdonald, D. W. (2012) Hedgerow trees and extended-width field margins enhance macro-moth diversity: implications for management. *Journal of Applied Ecology*, 49, 1396-1404

Met Office (2011) Driest March for years [Internet]. 31 March 2011. *Met Office News Blog*. Available from: http://blog.metoffice.gov.uk/ [Accessed 10 January 2016]

Moberg, F. (2010) Does biodiversity matter, and if it does how do we communicate it? Conference paper at: http://www.trondheimconference.org/. [Accessed Oct 2011]

Mohrig, W. and Blasco-Zumeta, J. (1995) The sciarid fauna (Diptera, Sciaridae) of a Juniperus thurijera L. forest of the Monegros region (Zaragoza, Spain) with description of ten new species. *Miscelanea Zoologica*, 18, 99-116

Mommertz, S., Schauer, C., Kösters, N., Lang, A. and Filser, J. (1996) A comparison of D-Vac suction , fenced and unfenced pitfall trap sampling of epigeal arthropods in agroecosystems. *Annales Zoologici Fennici*, 33, 117-124

Moore, N. W. (1968) Part III: Wildlife conservation and the hedgerow habitat. In: M. D. Hooper and M. W. Holdgate (Eds.) *Hedges and hedgerow trees*, Monks Wood Symposium No. 4, 25th – 26th November 1968, 53-57. Available from: http://nora.nerc.ac.uk/ [Accessed 28 April 2014]

Moreby, S. J. and Southway, S. (2001) The importance of hedgerow field boundaries to densities of beneficial invertebrates in cereals. In: C. Barr and S. Petit (Eds.) *Hedgerows of the World: their ecological functions in different landscapes*. Proceedings of the tenth Annual IALE (UK) Conference, held at Birmingham University, 5th – 8th September 2001, 213-218

Morris, M. G. (2000) The effects of structure and its dynamics on the ecology and conservation of arthropods in British grasslands. *Biological Conservation*, 95, 129-142

Morrison III, W. R., Waller, J. T., Brayshaw, A. C., Hyman, D. A., Johnson, M. R. and Fraser, A. M. (2012) Evaluating Multiple Arthropod Taxa as Indicators of Invertebrate Diversity in Old Fields. *The Great Lakes Entomologist*, 45, 56-67

Mossman, H. L., Franco, A. M. A. and Dolman, P. M. (2013) *Terrestrial biodiversity climate change impacts report card technical paper: 3. implications of climate change for UK invertebrates (excluding butterflies and moths)*. Norwich: UEA

Mouillot, D., Bellwood, D. R., Baraloto, C., Chave, J., Galzin, R., Harmelin-Vivien, Kulbicki, M., Lavergne, S., Lavorel, S., Mouquet, N., Paine, C. E. T., Renaud, J. and Thuiller, W. (2013) Rare Species Support

Vulnerable Functions in High-Diversity Ecosystems [Internet]. *PLoS Biology*, 11, e1001569. Available from: www.plosbiology.org [Accessed 05 July 2013]

Muir, R. (2000) *The NEW Reading the Landscape: Fieldwork in Landscape History*. Exeter: University of Exeter Press

Muir, R. and Muir, N. (1987) *Hedgerows: their history and wildlife*. London: Michael Joseph

Munro, N. T., Fischer, J., Wood, J. and Lindenmayer, D. B. (2009) Revegetation in agricultural areas: the development of structural complexity and floristic diversity. *Ecological Applications*, 19, 1197-1210

NFU (2013) *NFU Response – Proposed changes to AES Options*, 11 June 2013 [Internet]. Available from: www.nfuonline.com [Accessed 1 May 2014]

Narum, S. R. (2006) Beyond Bonferroni: Less conservative analyses for conservation genetics. *Conservation Genetics*, 7, 783-787

Natural England (2008) *Hedgerow trees: answers to 18 common questions* [Internet]. Available from: www.ptes.org [Accessed 5 November 2013]

Natural England (2009) *Agri-environment schemes in England 2009: A review of results and effectiveness* [Internet]. Available from: www.naturalengland.org.uk [Accessed 10 January 2013]

Natural England (2010) *Entry Level Stewardship Environmental Stewardship Handbook Third Edition – February 2010*. Available from: www.naturalengland.org.uk/publications [Accessed 10 January 2013]

Natural England (2012a) *Entry Level Stewardship: Environmental Stewardship Handbook, Fourth Edition – January 2013* [Internet]. Available from: http://publications.naturalengland.org.uk [Accessed 25 October 2013]

Natural England (2012b) *Higher Level Stewardship: Environmental Stewardship Handbook, Fourth Edition – January 2013* [Internet]. Available from: http://publications.naturalengland.org.uk [Accessed 25 October 2013]

Natural England (2012c) *Celebrating 25 years of agri-environment schemes* [Internet]. Available from: www.naturalengland.org.uk [Accessed 10 May 2013]

Natural England (2013) *Environmental Stewardship: Supplement for the 1st, 2nd & 3rd Edition HLS Handbook* [Internet]. Available from http://publications.naturalengland.org.uk [Accessed 25 October 2013]

Natural England (2015) Countryside Stewardship Manual. Available from: www.gov.uk/natural-england [Accessed 1 December 2015]

Natural England (no date a) *Research and Evidence: Land Management* [Internet]. Available from: http://www.naturalengland.org.uk/ourwork/research/landmanagement.aspx [Accessed 12 December 2011]

Natural England (no date b) Injurious weeds and invasive plants [Internet]. Available from: http://www.naturalengland.org.uk/ourwork/regulation/wildlife/enforcement/injuriousweeds.aspx [Accessed 10 May 2014]

Natural England (and Defra/Forestry Commission) (2015) *Countryside Stewardship grant: Planting new hedges (BN11)* [Internet]. Available from: https://www.gov.uk/ [Accessed 19 October 2015]

Natural England and RSPB (2014) *Climate Change Adaptation Manual* [Internet]. Available from: www.naturalengland.org.uk [Accessed 17 January 2016]

Nelder, J. A. and Wedderburn, R. W. M. (1972) Generalized Linear Models. *Journal of the Royal Statistical Society. Series A (General)*, 135, 370-384

New, T. R. (1970) The Relative Abundance of Some British Psocoptera on Different Species of Trees. *Journal of Animal Ecology*, 39, 521-540

New, T. R. (1996) Taxonomic Focus and Quality Control in Insect Surveys for Biodiversity Conservation. *Australian Journal of Entomology*, 35, 97-106

New, T. R. (1998) *Invertebrate Surveys for Conservation*. Oxford: Oxford University Press

New, T. R. (2005a) *Invertebrate conservation and agricultural ecosystems*. Cambridge: Cambridge University Press

New, T. R. (2005b) *Handbooks for the Identification of British Insects, Volume 1, Part 7: Psocoptera (booklice, barklice)*, 2nd edition. Preston Montford: Field Studies Council for the Royal Entomological Society

Nicolai, V. (1986) The bark of trees: thermal properties, microclimate and fauna. *Oecologia*, 69, 148-160

Nielsen, B. O. and Nielsen, L. B. (2007) Soil Diptera of a beech stand and an arable field: A comparison of dipteran emergence in neighbouring sites. *Pedobiologia*, 51, 33-43

Norris, K. (2010) Agriculture, woodland and semi-natural habitats. In: N. Maclean (Ed.) *Silent Summer: The State of wildlife in Britain and Ireland*, 22-35. Cambridge: Cambridge University Press

O'Hara, R. B. and Kotze, D. J. (2010) Do not log-transform count data. *Methods in Ecology and Evolution*, 1, 118-122

Obrist, M. K. and Duelli, P. (2010) Rapid biodiversity assessment of arthropods for monitoring average local species richness and related ecosystem services. *Biodiversity Conservation*, 19, 2201-2220

Office for National Statistics (2015) *National population projections, 2014-based Statistical Bulletin*, 29 October [Internet]. Available from: http://www.ons.gov.uk/ons/index.html [Accessed 27 November 2015]

Oldroyd, H. (1970) *Handbooks for the identification of British insects, Vol. IX, Part 1: Diptera, 1. Introduction and key to families* (Third edition, rewritten and enlarged). London: Royal Entomological Society of London

Oliver, T., Roy, D. B., Hill, J. K., Brereton, T. and Thomas, C. D. (2010) Heterogeneous landscapes promote population stability. *Ecology Letters*, 13, 473-484

Oecos (2009) *Sticky traps – wetstick* [Internet]. Available from: http://www.oecos.co.uk/sticky%20trap.htm [Accessed 07 January 2015]

Oosterbroek, P. (2006) *The European Families of the Diptera: Identification, diagnosis, biology*. Utrecht: KNNV Publishing

Ozanne, C. M. P. (1996) Arthropod communities of coniferous forest trees. *Selbyana*, 17, 43-49

Ozanne, C. M. P. (2005) Techniques and methods for sampling canopy insects. In: S. Leather (Ed.) *Insect Sampling in Forest Ecosystems*, 146-167. Oxford: Blackwell Publishing

Ozanne, C. M .P., Hambler, C., Foggo, A. and Speight, M. (1997) The significance of edge effects for the management of forests for biodiversity. In: N.E. Stork, J. Adis, R. K. Didham (Eds.) *Canopy Arthropods*, 535-550. London: Chapman & Hall

Ozanne, C. M. P., Anhuf, D., Boulter, S. L., Keller, M., Kitching, R. L., Körner, C., Meinzer, F. C., Mitchell, A. W., Nakashizuka, T., Silva Dias, P. L., Stork, N. E., Wright, S. J. and Yoshimura, M. (2003) Biodiversity Meets the Atmosphere: A Global View of Forest Canopies. *Science*, 301, 183-186

PTES (no date) *Hedgerows: a guide to wildlife and management*. Available from: www.ptes.org [Accessed 20 September 2013]

Paoletti, M. G. (Ed.) (1999) Invertebrate biodiversity bioindicators of sustainable landscapes. Practical use of invertebrates to assess sustainable land use. *Agriculture, Ecosystems and Environment*, 74, 1-444

Parker, G. G. (1995) Structure and microclimate of forest canopies. In: M. Lowman and N. Nadkarni (Eds.) *Forest canopies: a review of research on a biological frontier*, 431-455. San Diego: Academic Press

Pasek, J. E. (1988) Influence of wind and windbreaks on local dispersal of insects. *Agriculture, Ecosystems & Environment*, 22-23, 539-554

Pawson, S. M., Brockerhoff, E. G., Watt, M. S. and Didham, R. K. (2011) Maximising biodiversity in plantation forests: insights from long-term changes in clearfell-sensitive beetles in a *Pinus radiata* plantation. *Biological Conservation*, 144, 2842-2850

Pearce, J. L., Schuurman, D., Barber, K. N., Larrivee, M., Venier, L. A., McKee, J. and McKenney, D. (2005) Pitfall trap designs to maximize invertebrate captures and minimize captures of non target vertebrates. *Canadian Entomologist*, 137, 233-250

Peng, R. K., Sutton, S. L. and Fletcher, C. R. (1992) Spatial and temporal distribution patterns of flying Diptera. *Journal of Zoology*, 228, 329-340

Petit, S. and Burel, F. (1998) Connectivity in fragmented populations: *Abax parallelepipedus* in a hedgerow network landscape. *Ecology*, 321, 55-61

Petit, S. and Usher, M. B. (1998) Biodiversity in agricultural landscapes: the ground beetle communities of woody uncultivated habitats. *Biodiversity and Conservation*, 7, 1549-1561

Pinchen, B. J. (2005) A Pocket Guide to the Ladybirds of Britain and Ireland. Lymington: Forficula Books

Plant, C. W. (1994) *Provisional atlas of the lacewings and allied insects (Neuroptera, Megaloptera, Raphidioptera and Mecoptera) of Britain and Ireland*. Huntingdon: Biological Records Centre

Plant, C. W. (1997) A key to the adults of British lacewings and their allies (Neuroptera, Megaloptera, Raphidioptera and Mecoptera. *Field Studies*, 9, 179-269

Pocock, M. J. O., Chapman, D. S., Sheppard, L. J. and Roy, H. E. (2014) *A Strategic Framework to Support the Implementation of Citizen Science for Environmental Monitoring*. Final report to SEPA. Wallingford, Oxfordshire: Centre for Ecology & Hydrology

Pollard, E. (1968a) Hedges III: the effect of removal of the bottom flora of a hawthorn hedgerow on the Carabidae of the hedge bottom. *Journal of Applied Ecology*, 5, 125-139

Pollard, E. (1968b) Biological effects of shelter – interrelations between hedge and crop invertebrate fauna. In: M. D. Hooper and M. W. Holgate (Eds) *Hedges and Hedgerow Trees*. Monks Wood Symposium No. 4, 25th – 26th November, 39-46

Pollard, K. A. and Holland, J. M. (2006) Arthropods within the woody element of hedgerows and their distribution pattern. *Agricultural and Forest Entomolo*gy, 8, 203-211

Pollard, E., Hooper, M. D. and Moore, N. W. (1974) *Hedges*. London: Collins

Pollard, S. D., Jackson, R. R., Van Olphen, A. and Robertson, M. W. (1995) Dysdera crocata (Araneae, Dysderidae) prefer woodlice as prey? *Ethology Ecology and Evolution*, July, 271-275

Prather, C. M., Pelini, S. L., Laws, A., Rivest, E., Woltz, M., Bloch, C. P., Del Toro, I., Ho C. K., Kominoski, J., Newbold, T. A., Parsons, S. and Joern, A. (2013) Invertebrates, ecosystem services and climate change. *Biological Reviews*, 88, 327-348

Preisser, E.L**.**, Smith, D.C., and Lowman, M. D. (1998) Canopy and ground level insect distribution in a temperate forest. *Selbyana*, 19, 141-146

Prendergast, J. R. (1997) Species richness covariance in higher taxa: empirical tests of biodiversity indicator concept. *Ecography*, 20, 210-216

Primack, R. B. (2004) *A Primer of Conservation Biology*. Third Edition. Massachusetts: Sinauer Associates, Inc.

Proud, D. N., Felgenhauer, B. E., Townsend Jr., V. R., Osula, D. O., Gilmore III, W. O., Napier, Z. L., and Van Zandt, P. A. (2012) Diversity and Habitat Use of Neotropical Harvestmen (Arachnida, Opiliones) in a Costa Rican Rainforest. *International Scholarly Research Network ISRN Zoology,* Article ID 549765, 1-16

Pywell, R. F., James, K. L., Herbert, I., Meek, W. R., Carvell, C., Bell, D. and Sparks, T. H. (2005) Determinants of overwintering habitat quality for beetles and spiders on arable farmland. *Biological Conservation*, 123, 79-90

Pywell, R. F., Meek, W. R., Loxton, R. G., Nowakowski, M., Carvell, C. and Woodcock, B. A. (2011) Ecological restoration on farmland can drive beneficial functional responses in plant and invertebrate communities. *Agriculture, Ecosystems and Environment*, 140, 62–67

Quade, D. (1967) Rank analysis of covariance. *Journal of the American Statistical Association*, 62, 1187-1200

Quinlan, J. R. (1986) Induction of Decision Trees. *Machine Learning*, 1, 81-106

Quicke, D. L. (1997) *Parasitic wasps*. New York: Chapman & Hall

Rackham, O. (1976) *Trees and Woodland in the British Landscape*. London: Dent

Rackham, O. (1986) *The History of the Countryside*. London: Dent

Rahbek, C. (2012) *The biodiversity crisis: Worse than climate change*, 19 January [Internet]. University of Copenhagen News. Available from: http://news.ku.dk/all_news/2012/2012.1/biodiversity [Accessed 27 September 2015]

Rakotomalala, R. (2005) Arbres de décision [Decision Trees]. *Revue Modulad*, 33, 163-187

Rakotomalala, R. (no date) *Data Mining Links. Sipina Overview* [Internet page]. Available from: http://eric.univ-lyon2.fr/~ricco/sipina.html [Accessed 01 February 2013]

Ramankutty, N., Foley, J. A. and Olejniczak, N. J. (2002) People on the Land: Changes in Global Population and Croplands during the 20th Century. *Ambio*, 31, 251-257

Ravi, S., Crall, J. D., Fisher, A. and Combes, S. A. (2013) Rolling with the flow: bumblebees flying in unsteady wakes. *Journal of Experimental Biology*, 216, 4299-4309

Razali, N. M. and Wah, Y. B. (2011) Power comparisons of Shapiro-Wilk, Kolmogorov-Smirnov, Lillefors and Anderson Darling tests. *Journal of Statistical Modeling and Analytics*, 2, 21-33

Rehman, A. and Powell, W. (2010) Host selection behaviour of aphid parasitoids (Aphidiidae: Hymenoptera). *Journal of Plant Breeding and Crop Science*, 2, 299-311

Reid, C. and Grice, P. (2001) *English Nature Research Reports – Number 431: Wildlife gain from agri-environment schemes: recommendations from English Nature's habitat and species specialists.* Peterborough: English Nature

Resch, V. H. and Carde, R. T. (2003) *Encyclopedia of Insects*. San Diego: Academic Press/Elsevier
Rich, T. C. G., Clements, D. K., Lewis, J. and Moore, L. (2000) A comparison of four methods used to survey hedgerows: The Cardiff Hedgerow Survey 1998. *Journal of Environmental Management*, 60, 91-100
Richards, P. (2010) *Guide to harvestmen of the British Isles*. Shrewsbury: Field Studies Council
Richards, S. A. (2005) Testing ecological theory using the information-theoretic approach: examples and cautionary results. *Ecology*, 86, 2805-2814
Ricotta, C. (2005) Through the jungle of biological diversity. *Acta Biotheoretica*, 53, 29-38
Robacker, D. C. and Rodriguez, M. E. (2004) A Simple and Effective Cylindrical Sticky Trap for Fruit Flies (Diptera: Tephritidae). *Florida Entomologist*, 87, 492-495
Roberts, M. J. (1996) *Collins Field Guide: Spiders of Britain and Northern Europe*. London: HarperCollins
Robertson, J. (2014) Farming for nature – a return visit. *British Wildlife*, 25, 186-195
Robinson, G. (1998) Bugs, Hollow Curves and Species-diversity Indexes. *Stats*, 21, 8-13
Robinson, R. A. and Sutherland, W. J. (2002) Post-war changes in arable farmining and biodiversity in Great Britain. *Journal of Applied Ecology*, 39, 157-176
Rose, F. (2006) *The Wild Flower Key: How to identify wild flowers trees and shrubs in Britain and Ireland*. London: Penguin Group
Roth, D. S., Perfecto, I. and Rathcke, B. (1996) The Effects of Management Systems on Ground-Foraging Ant Diversity in Costa Rica. In: F. B. Samson and F. L. Knopf (Eds.) *Ecosystem Management*, 313-330. New York: Springer
Royal Entomological Society (2012) *Lacewings (Neuroptera)* [Webpage]. Available from: www.royensoc.co.uk/insect_info/what/lacewings.htm [Accessed 3 April 2013]
Rothamsted Research (2013) Rothamsted Insect Survey [Internet]. Available from: http://www.rothamsted.ac.uk [Accessed 11 November 2013]
RPA - Rural Payments Agency (2012) Cross compliance – Inspection Statistics [Internet]. Available from: www.rpa.gov.uk [Accessed 1 September 2012]
RPA - Rural Payments Agency (2013) Cross-compliance [Internet]. Available from: www.rpa.defra.gov.uk [Accessed 25 October 2013]
RSPB (2012a) Farm hedges: Value of hedgerows for wildlife [Internet]. Available from: www.rspb.org.uk [Accessed 25 October 2013]
RSPB (2012b) *London House Sparrows Parks Project* [Internet]. Available from: www.southwark.gov.uk [Accessed 11 March 2014]
Ruxton, G. D. and Beauchamp, G. (2008) Some suggestions about appropriate use of the Kruskal-Wallis test. *Animal Behaviour*, 76, 1083-1087
Samways, M. J. (2005) *Insect Diversity Conservation*. Cambridge: Cambridge University Press
Sandbrook, C. (2015) What is conservation? *Oryx*, 49, 565-566
Sankey, J. H. P. (1949) British harvest spiders. *Essex Naturalist*, 28, 181-191
Saville, R. E. (2010) An initial study of the feeding and egg-laying preferences of bark dwelling psocids (Psocoptera) using composite bark blocks. *Entomologists' Record and Journal of Variation*, 122, 35-42
Schmidt, M. H., Roschewitz, I, Thies, C. and Tscharntke, T. (2005) Differential effects of landscape and management on diversity and density of ground-dwelling farmland spiders. *Journal of Applied Ecology*, 42, 281-287
Shannon, C. E. and Weaver, W. (1949) *The mathematical theory of communication*. Urbana, Illinois: University of Illinois Press
Shaw, M. R. and Hochberg, M. E. (2001) The neglect of parasitic Hymenoptera in insect conservation strategies: The British fauna as a prime example. *Journal of Insect Conservation*, 5, 253-263
Shelef, O. and Groner, E. (2011) Linking landscape and species: Effect of shrubs on patch preference of beetles in arid and semi-arid ecosystems. *Journal of Arid Environments*, 75, 960-967
Sileshi, G. (2008) The excess-zero problem in soil animal count data and choice of appropriate models for statistical inference. *Pedobiologia*, 52, 1-17
Simpson, E. H. (1949) Measurement of diversity. *Nature*, 163, 688
Smith, H. G., Oeckinger, E. and Rundlöf, M. (2010) Biodiversity and the landscape ecology of agri-environment schemes. In: N. Boatman, M Green, J Holland, J Marshall, A Renwick, G Siriwardena, B

Smith and G de Snoo (Eds.) *Aspects of Applied biology 100, Agri-environment schemes – What have the achieved and where do we go from here?*, 225-232

Sobek, S., Kampichler, C. and Weigmann (2008) Oribatid mites (Acari, Pribatida) in the canopy of a Central European mixed forest: Species richness and species similarity between tree species and habitat types. In: A. Floren and J. Schmidl (Eds.) (2008) *Canopy arthropod research in Europe: Basic and applied studies from the high frontier,* 339-354. Nürnberg: Bioform

Sommaggio, D. (1999) Syrphidae: can they be used as environmental bioindicators? *Agriculture, Ecosystems and Environment*, 74, 343-356

Sotherton, N. W. (1984) The distribution and abundance of predatory arthropods overwintering on farmland. *Annals of Applied biology*, 105, 423-429

Sotherton, N. and Page, R. (1998) *A Farmer's Guide to Hedgerow and Field Margin Management*. Fordingbridge: The Game Conservancy Trust

Sotherton, N. W., Wratten, S. D., Price, S. B., White, R. J. (1981) Aspects of hedge management and their effects on hedgerow fauna. *Zeitschrift fur angewandte Entomologie*, 92, 425-432

Southwood, T. R. E., Brown, K. and Reader, P. M. (1979) The relationships of plant and insect diversities in succession. *Biological Journal of the Linnean Society*, 12, 327-348

Southwood, T. R. E. and Henderson, P. A. (2000) *Ecological Methods.* 3rd Edition. Oxford: Blackwell Science

Sparks, T. H., Hann, J .P. and Greatorex-Davies, J. N. (1999) The influence of field boundary structure on butterflies. *Aspects of Applied Biology*, 54, 235-240

Sparks, T. H., Parish, T. and Hinsley, S. A. (1996) Breeding birds in field boundaries in an agricultural landscape. *Agriculture, Ecosystems and Environment*, 60, 1-8

Speight, M., Hunter, M. D. and Watt, A. D. (1999) *Ecology of insects: concepts and applications*. Oxford: Blackwell Science

Spellerberg, I. F. and Fedor, P. J. (2003) A tribute to Claude Shannon (1916–2001) and a plea for more rigorous use of species richness, species diversity and the 'Shannon–Wiener' Index. *Global Ecology and Biogeography*, 12, 177-179

SPSS Inc. (no date) *Advanced Statistics 17.0* [Internet]. Chicago: SPSS Inc. Available from: http://www.spss.com [Accessed 20 April 2012]

Staley, J. T., Amy, S. R., Adams, N. P., Chapman, R. E., Peyton, J. M. and Pywell, R. F. (2015) Re-structuring hedges: Rejuvenation management can improve the long term quality of hedgerow habitats for wildlife in the UK. *Biological Conservation*, 186, 187-196

Staley, J. T., Amy, S, Facey, S. L. and Pywell, R. F. (2012a) Hedgerow Conservation and Management: A review of 50 years of applied research in the UK. In: J. Dover (Ed.) *Hedgerow Future*s: Proceedings of the first international Hedgelink Conference held at Staffordshire University, Stoke-on-Trent, UK, 3 - 5 September, 111-134. Leeds: Natural England

Staley, J. T., Sparks, T. H., Croxton, P. J., Baldock, K. C. R., Heard, M. S., Hulmes, S., Hulmes, L., Peyton, J., Amy, S. R. and Pywell, R. F. (2012b) Long-term effects of hedgerow management policies on resource provision for wildlife. *Biological Conservation*, 145, 24-29

Staley, J. T., Bullock, J. M, Baldock, K. C. R., Redhead, J. W., Hooftman, D. A. P., Button, N., and Pywell, R. F. (2013) Changes in hedgerow floral diversity over 70 years in an English rural landscape, and the impacts of management. *Biological Conservation*, 167, 97-105

Stelzl, M. and Devetak, D. (1999) Neuroptera in agricultural ecosystems. *Agriculture, Ecosystems & Environment*, 74, 305-321

Sterry, P. (2006) *Complete British Wild Flowers*. London: Harper Collins

Stewart, K. E. J., Bourn, N. A. D. and Thomas, J. A. (2001) An evaluation of three quick methods commonly used to assess sward height in ecology. *Journal of Applied Ecology*, 38, 1148-1154

Stoate, C., Boatman, N. D., Borralho, R. J., Carvalho, C. R., de Snoo, G. R. and Eden, P. (2001) Ecological impacts of arable intensification in Europe. *Journal of Environmental Management*, 63, 337-365

Stoate, C. (2014) Wildlife has its uses: Managing farmland for ecosystem services. *British Wildlife*, 25, 154-160

Stubbs, A. (2010) Flies, beetles and bees, wasps and ants (Diptera, Coleoptera and aculeate Hymenoptera). In: N. Maclean (Ed.) *Silent Summer: The State of Wildlife in Britain and Ireland*, 495-511. Cambridge: Cambridge University Press

Sustek, Z. (2008) Distribution of carabid beetles (Coleoptera, Carabidae) along a seminatural hedgerow in South Moravia. In: Muzeul Oteniei Craiova, Oltenia. *Studii si comunicari. Stiintele Naturii*, Tom. XXIV

Sutherland, W. J. (Ed.) (1996) *Ecological Census Techniques: a handbook*. Cambridge: Cambridge University Press

Sutherland, W. J. (Ed.) (2006) *Ecological Census Techniques: a handbook*. Second Edition. Cambridge: Cambridge University Press

Sutherland, W. J., Armstrong-Brown, S., Armsworth, P. R., Brereton, T., Brickland, J., Campbell, C. D., Chamberlain, D. E., Cooke, A. I., Dulvy, N. K., Dusic, N. R., Fitton, M., Freckleton, R. P., Godfray, H. C. J., Grout, N., Harvey, H. J., Hedley, C., Hopkins, J. J., Kift, N. B., Kirby, J., Kunin, W. E., Macdonald, D. W., Marker, B., Naura, M, Neale, A. R., Oliver, T., Osborn, D., Pullin, A. S., Shardlow, M. E. A., Showler, D. A., Smith, P. L., Smithers, R. J., Solandt, J-L., Spencer, J., Spray, C. J., Thomas, C. D., Thompson, J., Webb, S. E., Yalden, D. W. and Watkinson, A. R. (2006) The identification of 100 ecological questions of high policy relevance in the UK. *Journal of Applied Ecology*, 43, 617–627

Sutton, D. (1990) *Field guide to the trees of Britain & Europe*. London: Kingfisher Books

Symonds, M. R. E. and Moussalli, A. (2011) A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioural Ecology and Sociobiology*, 65, 13-21

Szeflinska, D. (2004) Thysanoptera community of midfield shelterbelts of different age. *Polish Journal of Ecology*, 52, 445-448

Tasker, J. (2009) One in four won't renew stewardship agreements [Internet]. *Farmers Weekly Interactive*, 20 August 2009. Available from: http://www.fwi.co.uk/Articles/2009 [Accessed: 1 April 2010]

TEEB (The Economics of Ecosystems and Biodiversity) (2010) *The Economics of Ecosystems and Biodiversity: Mainstreaming the Economics of Nature: A Synthesis of the Approach, Consultations and Recommendations of TEEB*. Available from: http://www.unep.org/pdf/LinkClick.pdf [Accessed 15 Sept 2015]

ter Braak, C. J. F. (1986) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology*, 67, 1167-1179

ter Braak, C. J. F. (1987) The analysis of vegetation-environment relationships by canonical correspondence analysis. *Vegetatio*, 69, 69-77

Texas A&M University (no date) *Cowpea weevil* [Internet]. Available from: https://insects.tamu.edu/fieldguide [Accessed 10 November 2013]

The World Bank (2015) *World Development Indicators*: Agricultural Land (% of Land area) [Internet]. Available from: http://databank.worldbank.org/data [Accessed 27 November 2015]

Thienemann, A. (1956) *Leben und Umwelt. Vom Gesamthaushalt der Natur*. Hamburg: Rowohlt

Thomas, C. F. G. and Marshall, E. J. P. (1999) Arthropod abundance and diversity in differently vegetated margins of arable fields. *Agriculture, Ecosystems and Environment*, 72, 131-144

Thomas, J. A. (2005) Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. *Philosophical Transactions of the Royal Society B*, 360, 339-357

Thomas, J. A. (2010) Butterflies. In: N. Maclean (Ed.) *Silent Summer: The State of Wildlife in Britain and Ireland*, 430-447. Cambridge: Cambridge University Press

Thomas, M. B., Wratten, S. D. and Sotherton, N. W. (1992) Creation of 'island' habitats in farmland to manipulate populations of beneficial arthropods, predator densities and species composition. *Journal of Applied Ecology*, 29, 524-531

Thomas, S. R., Goulson, D. and Holland, J. M. (2001) Resource provision for farmland gamebirds: the value of beetle banks. *Annals of Applied Biology*, 139, 111-118

Thomson, L. J., Neville, P. J., Hoffmann, A. A. (2004) Effective trapping methods for assessing invertebrates in vineyards. *Australian Journal of Experimental Agriculture*, 44, 947-953

Tilling, S. M. (1987) *A key to the Major Groups of British Terrestrial Invertebrates*. Field Studies Council, 187. Shrewsbury: Field Studies Council [Reprinted from *Field Studies*, 6, 695-766]

Tinker, J. (1974) The end of the English landscape. *New Scientist*, 64, 722-727

Todd, V. (1949) The habits and ecology of the British harvestmen. *Journal of Animal Ecology*, 18, 209-229

Toft, S. and Lovei, G. L. (2000) The epigeic spider fauna of single-row hedges in a Danish agricultural landscape. In: S. Toft and N. Scharff (Eds.), *European Arachnology 2000. Proceedings of the 19th European Colloquium of Arachnology*, Arhus, 17-22 July, 237-242

Tokeshi, M. (1993) Species abundance patterns and community structure. *Advanced Ecological Research*, 24, 112-186

Tovar-Sanchez, E. (2009) Canopy arthropods community within and among oak species in central Mexico. *Current Zoology*, 55, 132-144

Trigal-Domínguez, C., Fernández-Aláez, C. and García-Criado, F. (2010) Ecological assessment of highly heterogeneous systems: The importance of taxonomic sufficiency. *Limnologica - Ecology and Management of Inland Waters*, 40, 208-214

Trochim, W. M. K. (2006) *Research Methods Knowledge Base* [Internet]. Available from: http://www.socialresearchmethods.net [Accessed 10 January 2013]

Twiston-Davies, G., Mitchley, J. and Mortimer, S. (2011) *The Stonehenge Landscape Habitat Restoration Project: Conservation Opportunities For Rare Butterflies?* In: Vegetation Management. Association of Applied Biologists, 259-265

Ulrich, W. and Fiera, C. (2009) Environmental correlates of species richness of European springtails (Hexapoda: Collembola). *Acta Oecologica*, 35, 45-52

Ulyshen, M. D. (2011) Arthropod vertical stratification in temperate deciduous forests: implications for conservation-oriented management. *Forest Ecology and Management*, 261, 1479-1489

Unwin, D. (2001) *A Key to the Families of British bugs (Insecta, Hemiptera)*. Shrewsbury: Field Studies Council [Reprinted from *Field Studies*, 10, 1-35]

Unwin, D. M. (1988) *A Key to the Families of British Coleoptera (and Strepsiptera)*. Shrewsbury: Field Studies Council [Reprinted with minor alterations from *Field Studies*, 6, 149-197]

Unwin, D. M. (1981) A Key to the Families of British Diptera. *Field Studies*, 5, 513-533. Available for download from the Field Studies Council website: www.field-studies-council.org/fieldstudies/documents/vol5.3_143_A.pdf [Accessed 22 November 2011]

Usher, M. B. (1997) Biodiversity on agricultural land: habitats, species and hotspots. In: R. C. Kirkwood (Chair) *Biodiversity and conservation in agriculture, BCPC Symposium Proceedings No. 69. Proceedings of an international symposium held at The Stakis Brighton Metropole Hotel, 17 November 1997*, 1-14. Farnham: British Crop Protection Council

Veijola, H., Merilainen, J. J. And Marttila, V. (1996) Sample size in the monitoring of benthic macrofauna in the profundal of lakes: evlatuion of the precision of estimates. *Hydrobiologia*, 322, 301-315

Vickery, J. A., Feber, R. E., Fuller, R. J. (2009) Arable field margins managed for biodiversity conservation: A review of food resource provision for farmland birds. *Agriculture, Ecosystems & Environment*, 133, 1-13

Vinson, S. B. (1998) The General Host Selection Behavior of Parasitoid Hymenoptera and a Comparison of Initial Strategies Utilized by Larvaphagous and Oophagous Species. *Biological Control*, 11, 79-96

Wade, M. R., Gurr, G. M. and Wratten, S. D. (2008) Ecological restoration of farmland: progress and prospects. *Philosophical Transactions of the Royal Society B*, 363, 831-847

Walker (2011) *Featured creatures: house cricket* (*Acheta domesticus*) [Internet]. Available from: http://entnemdept.ufl.edu/creatures [Accessed 10 November 2013]

Wallwork, J. A. (1970) *Ecology of Soil Animals*. Maidenhead: McGraw-Hill

Wallwork, J. A. (1976) *The Distribution and Diversity of Soil Fauna*. London: Academic Press

Warwick, R. M. (1993) Environmental impact studies on marine communities: pragmatical considerations. *Australian Journal of Ecology*, 18, 63-80

Watt, T. A. and Buckley, G. P. (Eds.) (1994) *Hedgerow Management and Nature Conservation.* Wye College Press, Ashford

Weir, I. (no date) Spearman's rank correlation – Introduction [Internet]. Available from: www.statstutor.ac.uk [Accessed 8 May 2013]

West, T. M., Maudsley, M. J., Marshall, E. J. P. and Arnold, G. M. (1999) Restoring botanical diversity to degenerate hedge-bases. In: N. Boatman, D. H. K. Davies, K. Chaney, R. Feber, G. R. de Snoo and T. H. Sparks (Eds.) *Aspects of Applied Biology 54, Field Margins and Buffer Zones: Ecology, Management and Policy*, 251-256. Warwick: The Association of Applied Biologists

Wheater, C. P. and Cook, P. A. (2003) *Studying invertebrates*. Naturalists' Handbooks 28. Slough: The Richmond Publishing Co. Ltd

Wheater, C. P. and Cook, P. A. (2000) *Using Statistics to Understand the Environment*. Abingdon: Routledge

Wheater, C. P. and Read, H. J. (1996) *Animals under logs and stones*. Naturalists' Handbooks 22. Slough: The Richmond Publishing Co. Ltd

Whittingham, M. J. (2011) The future of agri-environment schemes: biodiversity gains and ecosystem service delivery? *Journal of Applied Ecology*, 48, 509-513

Whittingham, M. J. (2007) Will agri-environment schemes deliver substantial biodiversity gain, and if not why not? *Journal of Applied Ecology*, 44, 1-5

Williams, G. (1962) Seasonal and diurnal activity of harvestmen (Phalangida) and spiders (Araneida) in contrasted habitats. *Journal of Animal Ecology*, 31, 23-42

Williams, L.R. and Cunnington, W. (1985) Dating a hedgerow landscape in Middlesex: Fryent Country Park. *London Naturalist*, 64, 7-22

Wilson, E. O. (1987) The little things that run the world (the importance and conservation of invertebrates). *Conservation Biology*, 1, 344-346

Wilson, E.O. (1988) *Biodiversity*. Washington, DC: The National Academies Press

Wilson, R. (1979) The Hedgerow Book. Newton Abbot: David & Charles

Wissuwa, J., Salamon, J. A. and Frank, T. (2012) Effects of habitat age and plant species on predatory mites (Acari, Mesostigmata) in grassy arable fallows in Eastern Austria. *Soil Biology and Biochemistry*, 50, 96-107

Wollenberg, A. L. van den (1977) Redundancy analysis. An alternative for canonical correlation analysis. *Psychometrika*, 42, 207-219

Wolton, R. J. (2007) *Hedge-cutting: answers to 18 common questions*. Natural England

Wolton, R. J. (2010) *Local Hedgerow Survey Review, 2006-2008. A review of Defra-sponsored surveys carried out in 2006, 2007 and 2008 using the UK Hedgerow Biodiversity Action Plan standard procedure*. Report to Defra, on behalf of Hedgelink. Available from: www.hedgelink.org.uk. [Accessed 22 November 2011]

Wolton, R. J. (2011) *Environmental Stewardship and hedgerows: Briefing for change - Key facts, figures and pointers* [Internet]. Available from: www.hedgelink.org.uk [Accessed 2 December 2013]

Wolton, R., Morris, R., Pollard, K. and Dover, J. (2013) *Understanding the combined biodiversity benefits of the component features of hedges*. Defra: Contract number BD5214. Available from: www.hedgelink.org.uk [Accessed 20 April 2014]

Wolton, R. J. and Vergette, M. (2012) The diversity of life in a single hedge. In John W. Dover (Ed.) *Hedgerow Futures*: Proceedings of the first International Hedgelink Conference held at Staffordshire University, Stoke-on-Trent, UK, 3-5 September 2012, 98-104. Leeds: Natural England

Woodcock, B. A., Westbury, D. B., Potts, S. G., Harris, S. J., and Brown, V.K. (2005) Establishing field margins to promote beetle conservation in arable farms. *Agriculture, Ecosystems & Environment*, 107, 255-266

Woodland Trust (2013) *Lincolnshire* [Internet]. Available from: http://www.woodlandtrust.org.uk/en/campaigning/ [Accessed 19 June 2013]

Young, M. R. (2005) Insects in Flight. In: S.R. Leather (Ed.) *Insect Sampling in Forest Ecosystems*, 116-145. Oxford: Blackwell

Ysnel, F. and Canard, A. (2000) Spider biodiversity in connection with the vegetation structure and the foliage orientation of hedges. *Journal of Arachnology*, 28, 107-114

Zapparoli, M. (2011) New records and remarks on the centipede fauna of endogean habitats of Sardinia (Chilopoda). *Conservazione Habitat Invertebrati*, 5, 223-242

Zenner, E. K. (2004**)** Does old-growth condition imply high live-tree structural complexity? *Forest Ecology and Management*, 195, 243-258

Zhu, J. J., Matsuzaki, T. and Gonda, Y. (2003) Optical stratification porosity as a measure of vertical canopy structure in a Japanese coastal forest. *Forest Ecology and Management*, 173, 89-104

Zuur, A. F., Ieno, E. N. and Smith, G. M. (2007) *Analysing Ecological Data*. New York: Springer

Zwolfer, H. (1975) Speciation and niche diversification in phytophagous insects. *Verhandlungen der Deutschen Zoologischen Gesellschaft*, 67, 394-401

Appendix A. Supplementary information relating to Chapter 3

Table A1. Inventory of hedgerows and hedgeless boundaries investigated, giving basic details: location, type, identification code, estimated age, length, height and width

Location	Type	Hedge code (my identifier)	Age in 2011 (years)	Length (m) to nearest 5m	Height (m) to nearest 25cm	Margin Width (m) to nearest 25cm
Nettleham	Mature	N52	100	290	2.50	2.50
Nettleham	Mature	N59	100	275	2.00	1.50
Nettleham	Mature	NAd10	300	365	4.25	6.00
Nettleham	Mature	NEB3	100	290	2.50	2.75
Nettleham	New	N44	10	270	3.50	8.50
Nettleham	New	N46	10	390	2.00	2.75
Nettleham	New	N55	8	360	2.75	2.50
Nettleham	New	N58	9	455	2.00	2.25
Nettleham	New	N60	9	295	2.50	2.50
Nettleham	Hedgeless	NGB	N/A	65	N/A	7.00
Potterhanworth	Mature	P1709	200	155	3.50	2.25
Potterhanworth	Mature	PEB10	100	125	3.00	7.75
Potterhanworth	New	P13	10	90	2.50	6.00
Potterhanworth	New	P14	10	225	2.25	6.00
Potterhanworth	New	P33a	15	410	2.50	6.25
Potterhanworth	New	P33b	15	300	2.50	3.00
Potterhanworth	New	P57	8	105	2.75	3.25
Potterhanworth	New	P6	12	140	2.50	2.50
Potterhanworth	New	P63	10	155	2.75	5.50
Potterhanworth	New	P7	10	300	2.00	2.75
Potterhanworth	Hedgeless *	PBB	N/A	315	N/A	17.00
Riseholme	Mature	R13	100	470	3.00	3.50
Riseholme	Mature	R14	100	185	4.00	3.75
Riseholme	Mature	R23	100	460	3.00	3.00
Riseholme	Mature	R26	50	510	3.00	2.25
Riseholme	Mature	RA15	200	265	3.00	3.25
Riseholme	New	R17	6	140	2.75	2.75
Riseholme	New	R28	6	135	1.25	2.75
Riseholme	New	R4	6	215	2.75	2.00
Riseholme	Hedgeless	RWE	N/A	230	N/A	1.25
Swallow	Mature	S20	200	255	3.75	3.00
Swallow	Mature	S21	200	340	5.00	2.25
Swallow	Mature	S22	100	210	4.50	3.00
Swallow	Mature	S23	200	185	4.50	5.00
Swallow	Mature	S26	100	255	4.25	2.75
Swallow	Hedgeless	SGB	N/A	30	N/A	5.00

*Beetle Bank

I assigned my own identification codes to the hedges shown in Table A1, consisting of a letter followed by a number, where N = Nettleham, P = Potterhanworth, R = Riseholme and S = Swallow, and the number coincides with numbers from stewardship maps in the case of the hedgerows. Coding for the hedgeless grassy boundaries consists of a location code as above plus a combination of letters describing the habitat, where GB = grassy border, BB = Beetle bank and WE = woodland edge. Where a numbered stewardship map was not obtained for Swallow numbers were assigned according to a sequence used during a walk over of the farm site to identify suitable hedgerows.

A1. Laboratory work on sticky trap selection

Laboratory work was undertaken specifically to select the appropriate materials for sticky trapping on hedgerows. It was considered that the traps should have the best adhesive qualities, capable of trapping a range of differently sized, and both weaker and stronger invertebrate fauna.

A1.1. Methodology for laboratory-based pilot studies of sticky traps

A range of sticky trap designs were tested, including commercially available pest control and monitoring products and 'home-made' traps. The traps tested were: Aphid traps (Time's up Insect Catcher™ by STV International), Cockroach traps (Zero In™ by STV International), Fly traps (Advanced Fly Trap Window Stickers by Rentokil), and improvised traps using Oecotak™ (Oecos) and strong 'gaffer'/duct tape (B&Q own brand). Tests were set up for each of the five alternative sticky substances, using adult *Callosobruchus maculatus* beetles (~3mm long)[20], larval mealworms (range of instars) (*Tenebrio molitor*) and adult crickets[21] (*Acheta domesticus*) to represent a range of sizes and mobility of invertebrates. Data were collected on capture rates in order to determine the efficiency of the sticky surfaces in catching different invertebrates.

Steps taken in conducting the experiment were as follows:

1) For each set of tests plastic sandwich boxes were used as containers , each measuring 22.5 x 9.5 x 5 cm (length x width x height), although in principle boxes of any dimensions, provided they were all equal size, could have been used. This particular box was selected for its low cost and availability. Five replicates were tested for each of the 5 trap types and each of the three experimental animals consecutively.
2) Population of experimental animals (*Callosobruchus maculatus,* larval forms of *Tenebrio molitor* and *Acheta domesticus* respectively for experiments *1, 2 and 3)*
3) All sticky pads were cut to a uniform size of 10 x 6cm.
4) One sticky pad was placed flat in the centre of each sandwich box.
5) Test animals were introduced into each box, although not directly onto the sticky pad, before closing the lid. Ventilation holes had been cut into the lids.

[20] Source: Texas A&M University (no date)
[21] Adults range between 16 – 21 mm (Walker, 2011)

6) Boxes were kept for 24 hours under controlled conditions in the University insectary, which was maintained at 27 – 30 ^{0}C, with relative humidity between 25% and 35% and a 16:8 hr light: dark photo period.
7) After a period of 24 hours contents of the boxes were inspected to check how many of the test animals had been trapped on the sticky pads.
8) The numbers of individuals trapped and free-moving were recorded.
9) The used sticky pads and their contents, plus remaining untrapped individuals were removed from the boxes and placed in plastic sealed bags and transferred to a freezer to kill off any living individuals and for storage.

A1.2. Results of laboratory-based pilot studies of sticky traps

The Cockroach trap trapped and retained higher numbers of animals than alternative sticky trap materials (Figs. A1 (a)–(d)). Results of experiment #1 using *Callosobruchus maculatus* indicate that the cockroach trap was the most effective at trapping animals (Fig. 3.7(a)). A Kruskal-Wallis test showed a statistically highly significant difference between the trap types: $H_{(4)} = 18.85$, $p = 0.001$. As a means of making post-hoc multiple comparisons SPSS provides pairwise comparisons of the mean rank of each trap type. In this case, these comparisons show a significant difference in mean rankings only between the cockroach traps and the gaffer tape traps ($p < 0.001$).

The results of experiment #2 using larval *Tenebrio molitor* (Fig. 3.7(b)) and again show the Cockroach trap to be the most effective at trapping animals. A Kruskal-Wallis test indicated a statistically significant difference between the trap types: $H_{(4)} = 16.12$, $p = 0.003$. The post-hoc rank comparisons showed that there were significant differences between the Cockroach trap and the Fly trap ($p = 0.01$) and the Cockroach trap and the Aphid trap ($p = 0.005$).

Figure 3.7(c) shows the results of experiment #3 using *Acheta domesticus* where the Cockroach trap again comes out on top. Kruskal-Wallis tests indicated a statistically significant difference between trap types: $H_{(4)} = 16.65$, $p = 0.002$. Post-hoc comparisons of average rankings showed significant differences between the Gaffer tape trap and the Aphid trap ($p = 0.012$) and the Gaffer tape trap and the Cockroach trap ($p = 0.002$).

Figure 3.7(d) shows results from all three experiments combined, with the count numbers converted into % of animals trapped. The counts derived from summing results from the experiments conformed to a normal distribution (according to a Shapiro-Wilk test and Q-Q plots) and so a parametric comparison on these data was performed using a one-way ANOVA, to determine whether there were differences between numbers of animals trapped overall. A post-hoc multiple pairwise comparison test was used to determine where the differences lay. An ANOVA on the combined abundances from tests for all 3 taxa indicated that Cockroach traps captured highly significantly larger numbers of organisms overall than any other trap type: $F_{4, 20} = 46.64$, $p = < 0.001$ and Tukey HSD: $p = < 0.001$ (see Table A2 for the results of multiple comparisons between

trap types). No other comparisons between trap types were statistically significant and are not presented here. On the basis of these experiments, the commercially available Cockroach trap with the strongest adhesion was selected for further use in surveying in preference to the other sticky alternatives.

Table A2. Results of Tukey HSD post-hoc tests showing pairwise comparisons of Cockroach traps and other sticky trap types from laboratory work

Trap type		*p*	95% Confidence Interval	
			Lower Bound	Upper Bound
Cockroach versus	Aphid	<0.001	9.05	18.95
	Fly	<0.001	8.85	18.75
	Gaffer tape	<0.001	17.05	26.95
	OekoTak	<0.001	5.05	14.95

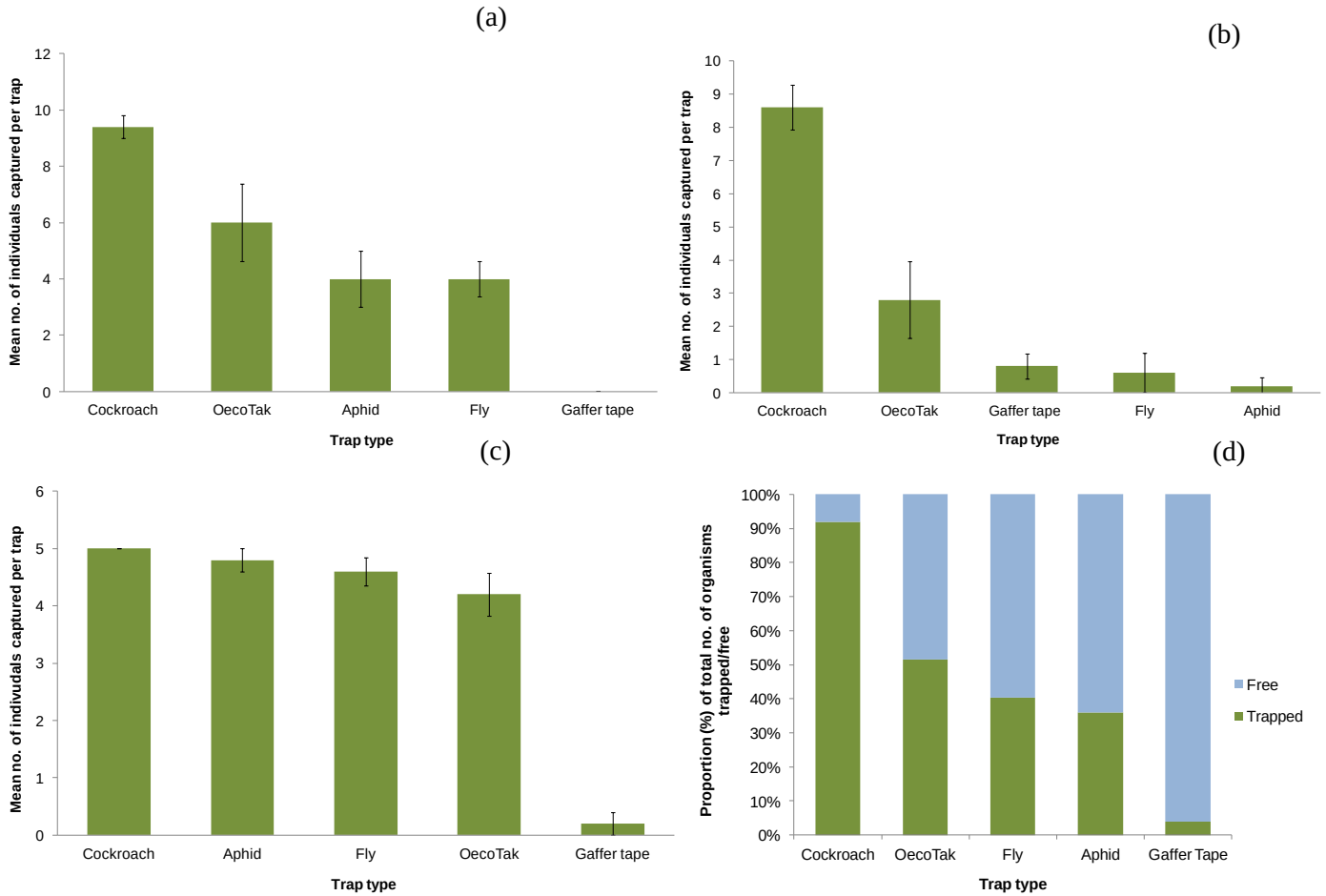


Figure A1. Comparison of the sticky trap effectiveness of 5 different types of sticky trap (Cockroach, Aphid, Fly, OecoTak, Gaffer tape) for collecting invertebrates. Mean numbers (± SE) of: (a) *Callosobruchus maculatus* (n = 10) caught after 24 hours per replicate (n = 5); (b) *Tenebrio molitor larvae* (n = 10) caught after 24 hours per replicate (n = 5); (c) *Acheta domesticus* (n = 5) caught after 24 hours per replicate (n = 5). Chart (d) compares the totals of all organisms for all taxa combined, trapped versus organisms untrapped, expressed as % proportions of the whole for each trap type

A2. Field work on sticky trap selection

A2.1. Pilot study of sticky trapping in the hedge bottom and hedge top #1

The effectiveness of sticky traps for sampling invertebrates in the hedge bottom was tested outdoors 'in the field' at both ground level and canopy level in the hedgerows. The original intention in my study was to use the sticky sampling technique in both the hedge bottom and hedge top, in order to be able to make direct comparisons between the invertebrate abundance and diversity of the two hedgerow components. The results of pilots of the sampling efficiency of sticky traps at both the canopy and ground level dissuaded me from using sticky trapping at canopy level.

Figures A2 (a) and A2 (b) below show the results of a pilot of sticky trapping at hedge top and hedge bottom respectively, conducted in July 2010. A total of 20 caged sticky traps were set at ground level in the hedge bottom of a mature hedgerow. The traps were placed at 2m intervals and within 1m of the centre of the hedge along a transect centred on a point midway between either end of the length of hedgerow. In addition, a total of 20 sticky traps (with protective mesh) were hung in the canopy of the hedgerow at approximately 1.5m above ground in order to sample invertebrate taxa active at hedgerow canopy level.

The results of this trial showed that using sticky traps at canopy level captured both a lesser abundance and a much lower diversity of taxa, than using sticky traps at ground level. Paired t tests were conducted on the normally distributed abundance and taxon richness data (according to Shapiro Wilks) and showed highly significant differences between the abundance and taxon richness of canopy-active versus ground-active invertebrates (t = 6.34, p = <0.001 and t = 8.067, p = <0.001 respectively). Shannon H' diversity values were not normally distributed and so were tested using a Wilcoxon Signed Rank test with the result that a highly significant difference was also shown between H' of hedge top and hedge bottom (Z = -3.88, p = <0.001).

Ground sticky traps were dominated by Acari (mites) and Hemiptera (bugs). Overall the catches were dominated by large numbers of small invertebrates; Acari, for instance, are generally <1mm. This may be a result of caging the traps to prevent by-catch, although the presence of a number of larger-bodied species, including Coleoptera, indicates that the caging did not entirely exclude larger individuals. The beetles were from a range of families, with predacious species Carabids (ground beetles), Staphylinids, Coccinellidae represented. Hymenoptera were represented largely by members of the large group of often very small parasitic wasps.

Hanging sticky trap catches were dominated by Hemiptera (represented largely by Aphididae) and Thysanoptera, with small numbers of tiny Hymenoptera ('Parasitica'). Organisms known to be present in aerial woody environments, such as Psocoptera (barkflies), were absent from the sticky traps in the canopy. This was considered to be an effect of sampling method rather than a true reflection of the invertebrate fauna living in the canopies of farmland hedgerows, when

compared with other studies, *e.g.* Pollard & Holland (2006) who used a fogging technique collected hundreds of barkflies.

A2.2. Pilot study of sticky trapping in the hedge bottom and hedge top #2

In addition to the July sampling, a further test of sticky trapping at both hedge bottom and in the hedge canopy was conducted in September 2010 on a Mature hedge (~100 years) and a New hedge (~5 years). A total of 25 traps were placed at the hedge bottom and 25 in the hedge canopy of each hedge and left for periods of increasing duration. These data were also used to determine the length of sampling sessions by generating taxon accretion curves (see Section 3.7 of Chapter 3. General Methodology). Selected results of this study only are presented here (Figs. A3. (a) and (b)). Results from the hedge bottom only are shown. Results from the canopy are not presented due to the lack of invertebrates collected: only 5 invertebrates were sampled in total using sticky traps at canopy level in the Mature hedge and a total of 109 in the New hedge (70% of which were Dermaptera).

On the basis of these results, showing such a paucity of organisms and taxa, sticky trapping at canopy level was rejected in favour of beating. As indicated, this followed consideration of other techniques during desk research. While beating using a funnel technique (as described in section 3.6 of thesis) did not yield a substantially greater number of organisms from the hedgerow than sticky traps, a trial sampling of the canopies of a range of hedgerows suggested that a much greater diversity of taxa could be collected (Fig. A2 (a), Fig. 3.14). Beating as a method of sampling invertebrates from the woody part of the hedge is discussed in further detail in section 3.6 of Chapter 3 General Methodology of the thesis.

A2.3. Pilot study comparing pitfall trapping with sticky trapping

A comparison between the effectiveness of sticky trapping and pitfall trapping, more conventionally used at ground level, was also made. The abundance, taxon richness and Shannon *H*' diversity of ground-active invertebrates sampled by three different types of trap (sticky trap, pitfall trap with antifreeze and pitfall trap with water) were compared. Five of each of the three trap types were positioned alternately at equidistant intervals of 2m along the central section of a mature hedgerow and left in situ for a 48-hour period from 25 to 27 August 2010. A 48-hour period was chosen because this had been used in previous work by me at undergraduate level using pitfall traps only to sample hedgerows on University of Lincoln farmland (Deeming *et al*., 2010). Some of the hedgerows used in the previous work were included in my thesis work and the aim was to produce data comparable with the earlier study.

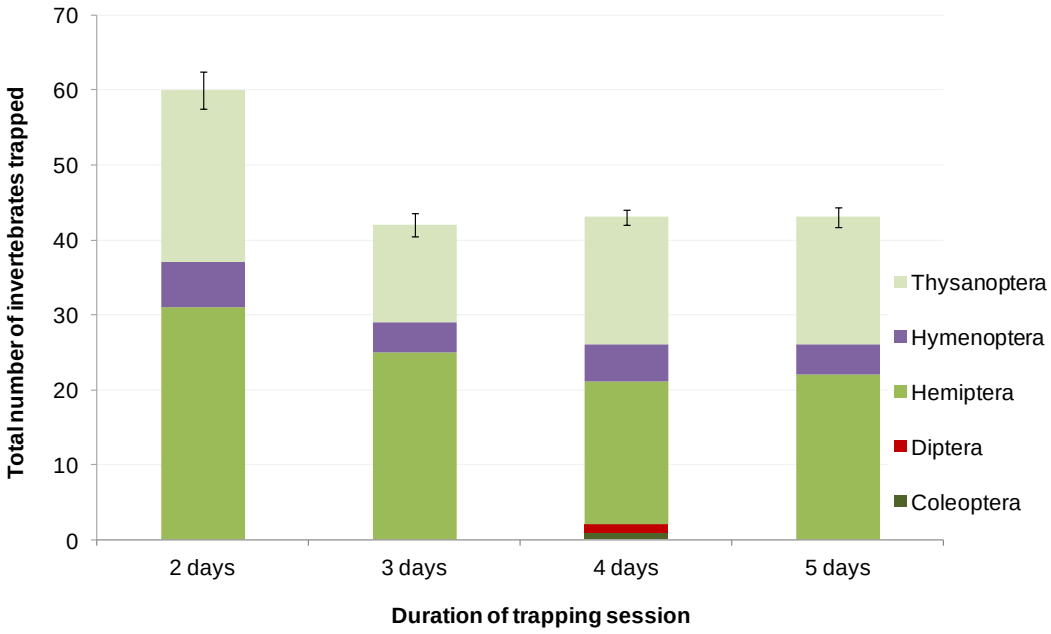
The abundance and diversity of hedge bottom invertebrates sampled using sticky traps were demonstrably different from the abundance and diversity of invertebrates sampled by pitfall trapping (Fig. A4), illustrating the fact that the trapping techniques sample different 'fractions' of

invertebrate diversity. Overall the abundance of invertebrates captured by sticky trap was much smaller, but the taxonomic richness (*i.e.* number of major invertebrate taxonomic groups sampled) and the diversity, measured using the Shannon index (*H*'), were both higher than produced by the pitfall traps.

Figure A4 illustrates the results of the 2-day pilot conducted in August 2010 comparing the effectiveness of sticky traps with pitfall traps of two different types: one set containing anti-freeze and one set containing water only. Pitfalls with anti-freeze caught the highest number of invertebrates and sticky traps markedly lower numbers of organisms overall compared with both types of pitfall trap. A one-way ANOVA showed that there was a significant difference between the abundance of invertebrates caught by the respective traps ($F_{2,12} = 12.833$, $p = 0.001$). Post-hoc Tukey HSD tests showed that there was a significant difference between sticky traps and both pitfalls with anti-freeze ($p = 0.001$) and pitfalls with water ($p = 0.10$). By contrast there was no significant difference between the two pitfall trap types.

The Shapiro-Wilk test and Q-Q plots show that the taxon richness data was not normally distributed and therefore a non-parametric test, Kruskal-Wallis, was used to compare the results. This showed no significant difference between the taxon richness of the 3 trap types ($H_{2,12} = 3.657$, $p = 0.161$). An ANOVA showed that there was also no significant difference between the Shannon diversity index (*H*') values of the invertebrate samples ($F_{2,12} = 2.699$, $p = 0.108$). However, sticky traps achieved the highest *H*' values of the three trap types: *H*' = 1.93, versus 1.69 and 1.56 for the pitfall traps with anti-freeze and with water respectively.

(a)



(b)

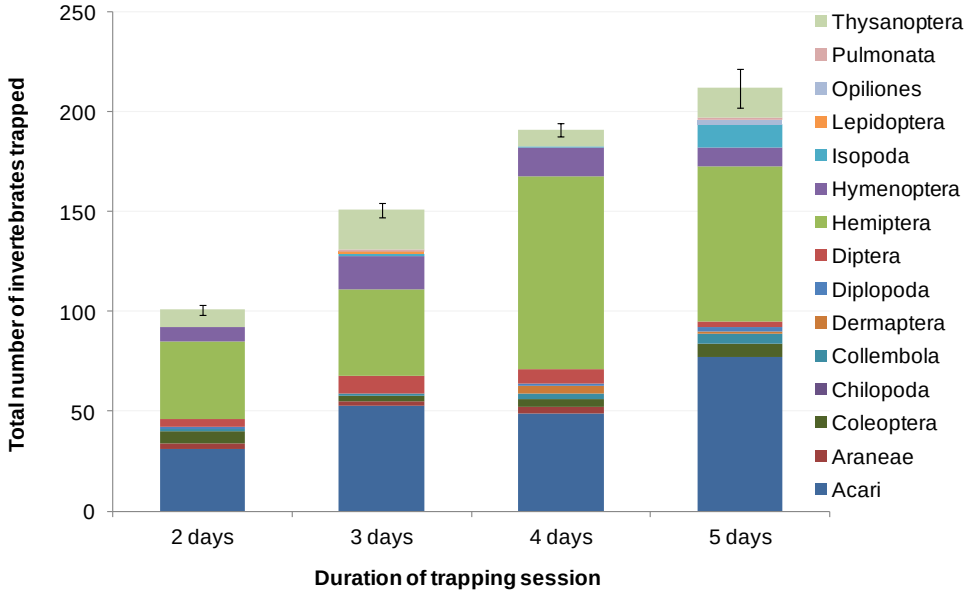
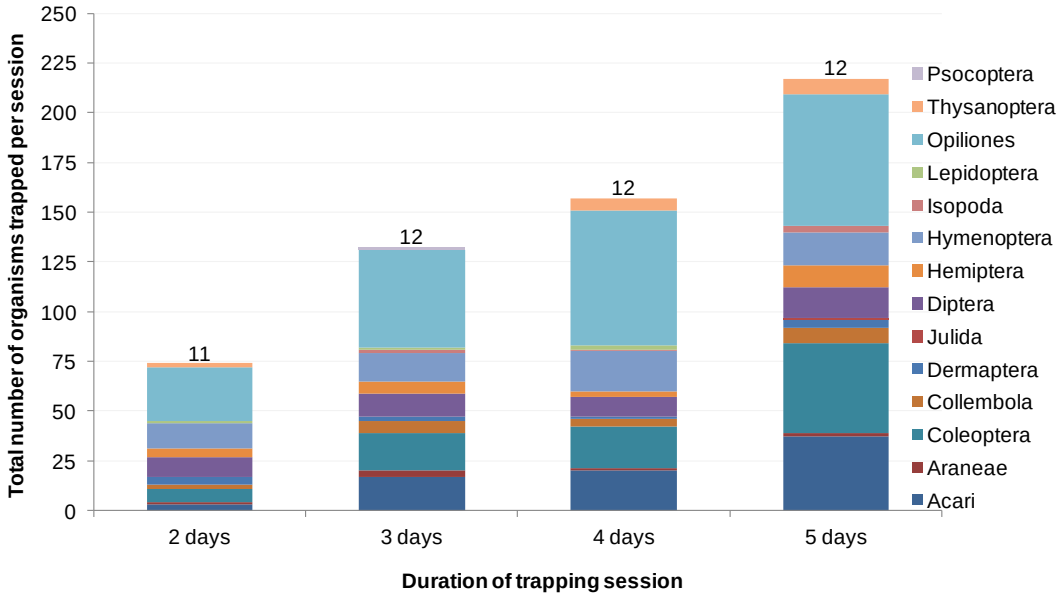


Figure A2. Results of a pilot study conducted in July 2010 showing the composition of invertebrate samples obtained by sticky trap (n = 5 per session) from a sample Mature hedgerow during trapping sessions of increasing duration (2, 3, 4 and 5 days): (a) by hanging in the hedge canopy; (b) by placing at hedge bottom. Bars represent ±SE

(a)



(b)

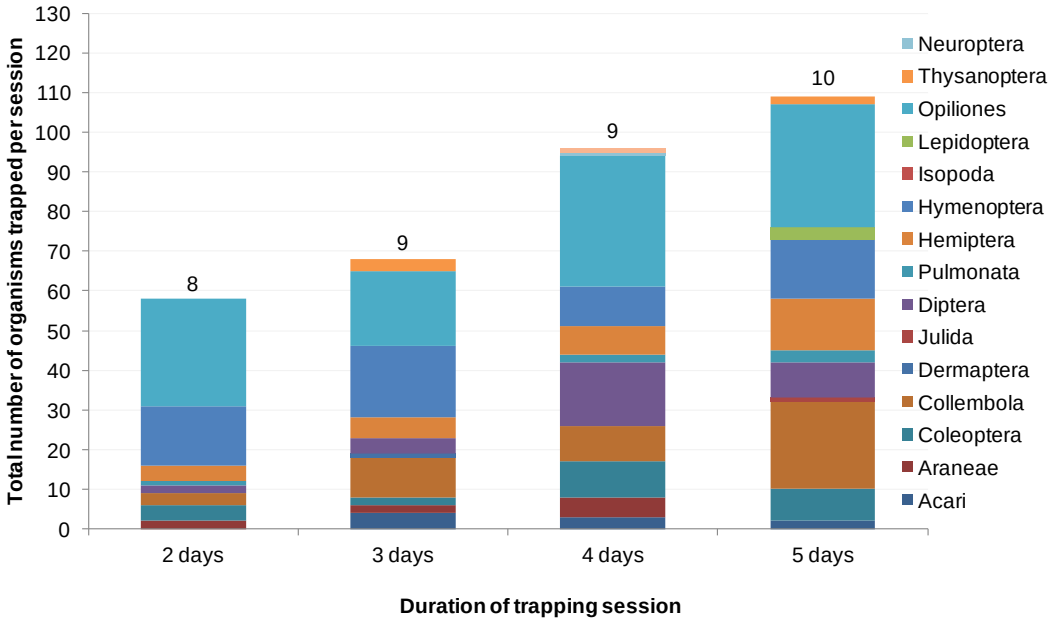


Figure A3. Results of a pilot study conducted in September 2010 comparing the composition of ground-level sticky trap catches for trapping sessions of different durations at the hedge bottom of: (a) R13, a Mature hedge of ~100 years, and (b) R17, a New hedge of ~5 years). Columns show the total abundance of invertebrates trapped for each session of increasing duration: 2 days, 3 days, 4 days, 5 days (n = 5 traps per session). Numbers above each column indicate the total number of invertebrate taxa caught per session

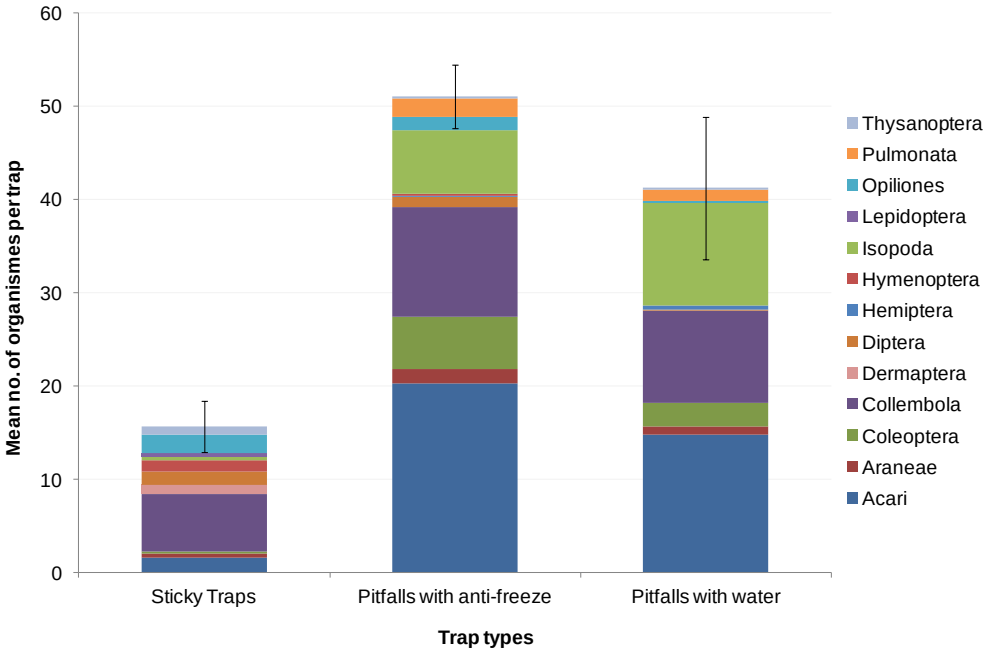
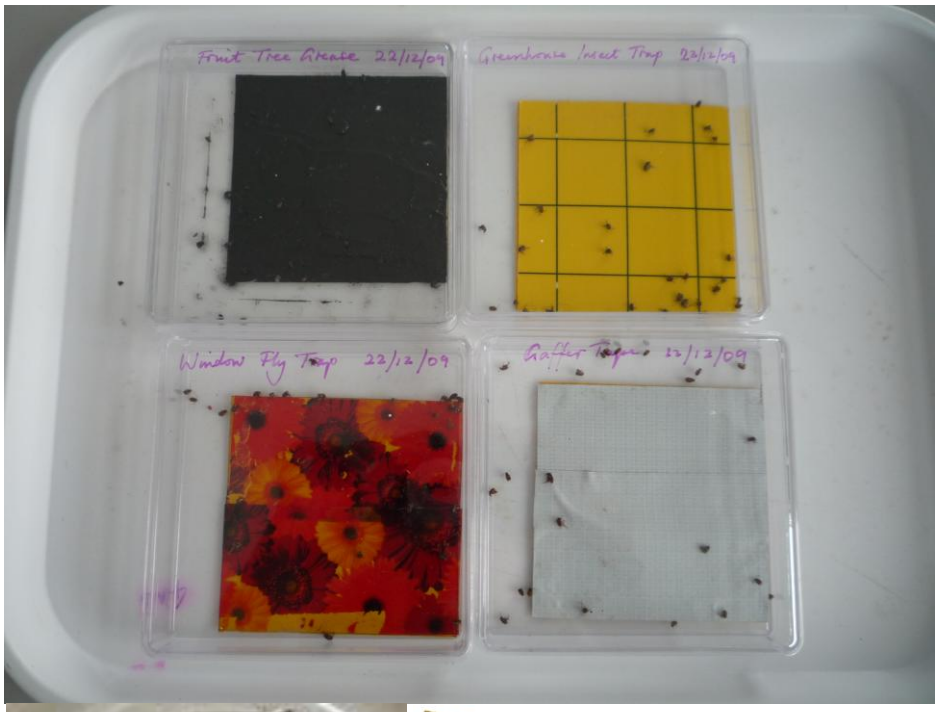


Figure A4. Results of a pilot study comparing the mean invertebrate abundance and diversity (number of taxa) of hedge bottoms sampled by three different types of trapping: sticky traps, pitfall traps containing anti-freeze and pitfalls containing water only. Stacked columns show the mean number of organisms trapped per trap type (n = 5 per trap type). Bars represent ±SE. Samples collected August 2010 over a 48 hour period

Figure A5 (a)–(e). Illustrations of different types of sticky trap trialled in the laboratory: (a) preliminary trial using Vitax Tree Grease, Greenhouse Insect Traps, Window Fly Traps and Gaffer Tape to trap *Callosobruchus maculatus*; (b) trap using Oekotak A5 with *Tenebrio molitor* larvae shown; (c) commercially available Window Fly Trap; (d) commercially available Gaffer tape; (e) commercially available Time's Up Greenhouse Insect Catcher

(a)



(b)

(c)

(d)

(e)

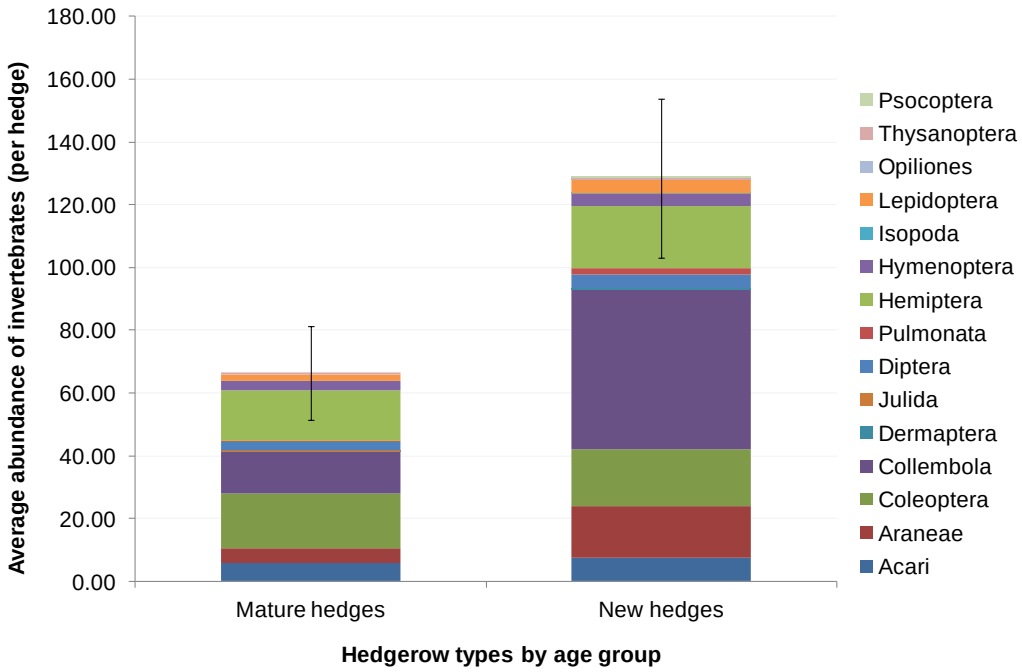


Figure A6. Results of a pilot study comparing the abundance and invertebrate composition of samples taken from Mature (n=10) and New (n=10) hedgerows, using a beating technique with a 28cm diameter funnel. Standard Error (±SE) is shown. Samples collected May 2010

A3. Pilot study to determine the effectiveness of beating for collecting invertebrates from the hedge canopy

Preliminary work on sampling hedge canopy invertebrates was undertaken in May 2010, using the beating technique described in Section 3.7 of the General Methodology (Chapter 3). The original 28cm diameter funnel was used in this work, but caught only relatively low mean numbers of invertebrates per hedgerow (Fig. A6). This seemed to be dependent on hedge age group, with Mature hedgerows yielding markedly fewer invertebrates (ranging between 17 and 170 per hedge) compared with New hedgerows (with numbers ranging between 54 and 314 per hedge).

A3.1. Increasing the effectiveness of the beating technique

Due to relatively small invertebrate catches obtained using the 28cm diameter funnel (Figs. A6 and A7), enlargement of the funnel was undertaken and tested prior to use in the 2011 data collection. Hence, in July 2010, a comparative study of the two funnel sizes and their effectiveness in sampling hedgerow invertebrates was undertaken. To this end, the canopy of R13, a mature hedge on the Riseholme estate, was sampled using the adapted beating technique – using a jarring stick to tap invertebrates via a reusable plastic funnel directly into a cylindrical plastic storage container. Two funnel sizes were used: 28cm diameter funnel and a 50cm funnel, adapted using a so-called Elizabethan surgical collar for dogs (the largest size available), attached to a 28cm funnel using gaffer tape.

Beatings were carried out using a folded 1m plastic measuring stick as a beating implement to beat and jar the lower canopy (c. 1m above ground) for 10 strikes at each sampling point. These beatings were carried out at sampling points at 4m intervals along a length of the hedgerow alternating between the 28cm and 50cm funnels. Eight samples per funnel size were taken.

The larger (50cm) funnel enabled the capture of both a greater abundance (69 versus 39 for the 28cm funnel, representing a 43% increase) and a greater Shannon diversity of invertebrates, *i.e.* *H*' = 1.734 for the larger diameter funnel versus *H*' = 1.575 for the smaller funnel (Fig. A7). Taxonomic richness was also higher in the 50cm sample with 9 taxa represented in total as opposed to 7 taxa in the 28cm sample (representing a 28% increase).

Enlarging the funnel and thereby increasing the area of the canopy sampled has the effect of boosting sampling area and effort with an effect on both the abundance and diversity of invertebrates caught. Both the number and the diversity of animals captured increased. While the enlarged funnel still delivered a relatively small sample size, it was considered a large enough improvement on numbers to be worth adopting. The diameter of the funnel was limited by availability of materials and issues of portability and so no further enlargements were made to attempt to further increase sampling effectiveness.

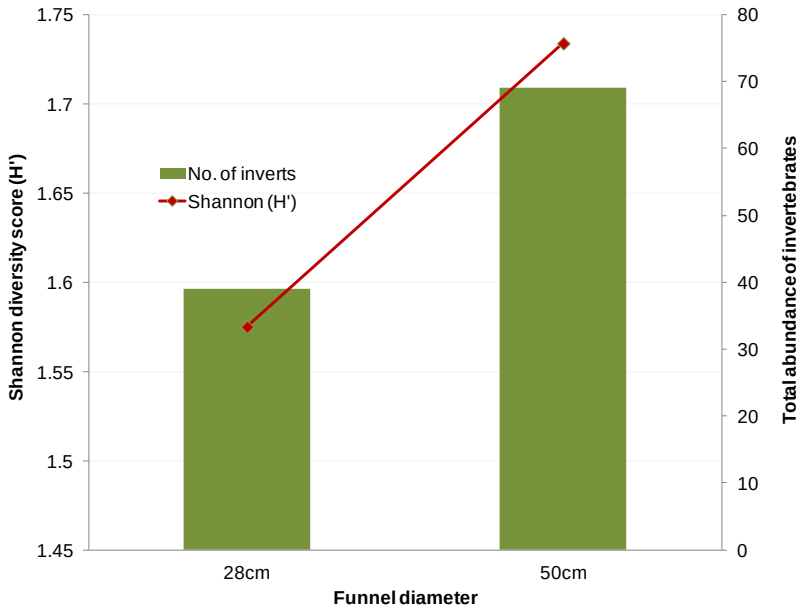


Figure A7. Comparison of total invertebrate abundance and diversity (Shannon *H*') from beatings with funnels of different diameters (28cm versus 50cm). Samples taken from one Mature hedge from equal numbers of alternating sampling points (n = 8) per funnel diameter. Beating was conducted in July 2010

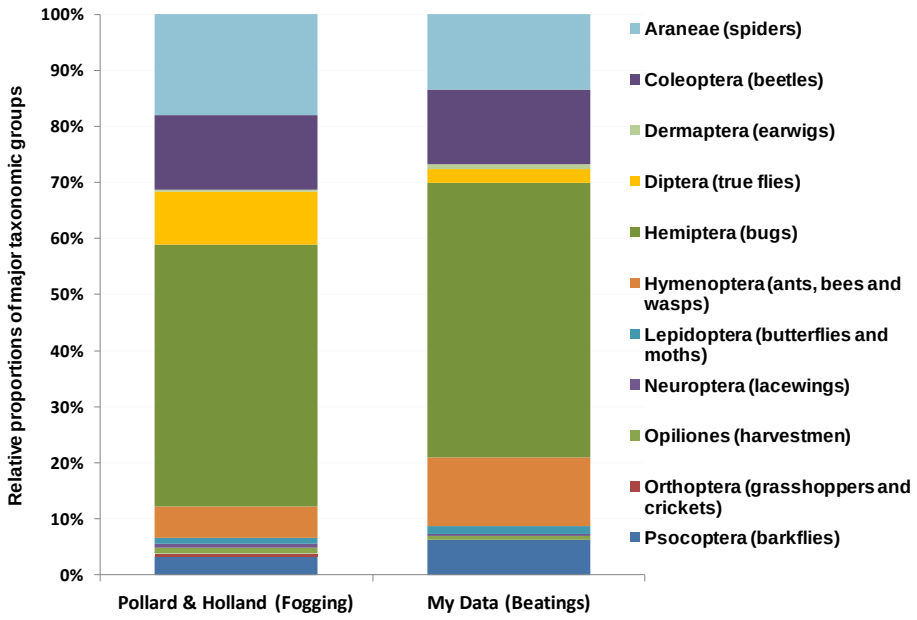


Figure A8. Relative proportions of selected major invertebrate groups collected from established farmland hedgerows by two techniques: fogging (n = 13) versus beating (n = 15). Month of sampling July (different years)

A4. Relative effectiveness of fogging versus adapted beating technique

Regarding the comparative effectiveness of fogging versus my beating technique, a direct comparison is not possible due to differences in sampling regimes, dates and locations of sampling, however for illustrative purposes a comparison has been made between the respective numbers and the make-up of the samples obtained (Fig. A8). Pollard & Holland (2006) collected 13,000 invertebrates from 13 hedgerows as opposed to 1,900 from 15 Mature hedges. There was a significant difference between the absolute capture rates of the two techniques in terms of numbers of invertebrates collected (Mann Whitney $U = 26.00$, $p = 0.023$) , but, interestingly, there was no difference in terms of the relative proportions (in %) of the main taxonomic groups represented in the catches by the two techniques: Mann Whitney $U = 60.00$, $p = 0.974$. Therefore, the assemblages sampled by both techniques appeared very similar in basic structure. This suggests comparable efficacy of my beating technique in measuring the diversity of major invertebrate groups within the hedge tops.

Table A3. Efficiency of different numbers of traps in sampling invertebrate taxa. Efficiency expressed in terms of % of original catch (no. of major taxonomic groups sampled using 10 traps) obtained by reduced effort. Based on % taxon accretion of invertebrate samples collected during May, July and September 2007 pitfall trapping of 6 farmland hedges

Month	Trapping Efficiency (% accretion of taxa)	Number of samples/traps required per hedge						
		Hedge A	Hedge B	Hedge C	Hedge D	Hedge E	Hedge F	Mean
May	80%	3	2	5	3	5	4	4
	90%	4	6	7	5	7	8	6
	95%	6	7	9	7	9	9	8
July	80%	3	5	7	4	4	4	5
	90%	6	8	9	7	6	5	7
	95%	8	9	9	9	8	7	8
Sept	80%	4	4	3	3	2	2	3
	90%	7	7	6	5	5	3	6
	95%	9	8	8	7	7	6	8

NB. All sample numbers have been rounded up to the nearest whole number.

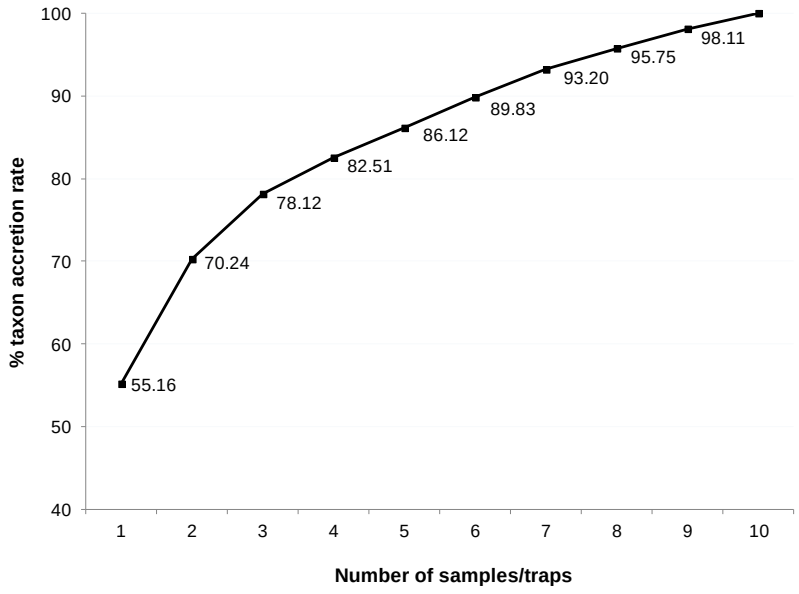


Figure A9. The mean taxon accretion rate (%) for May, July and September 2007 pitfall trapping

Appendix B. Supplementary information relating to Chapter 4

Table B1. Overview of the abundance (total by hedge type) and frequency of individual invertebrate taxa, for Mature and New hedges and Hedgeless boundaries (n) over time (Month: April, July, September). Frequencies of absent, 'singleton' and 'doubleton' taxa are shown. Invertebrates collected by sticky trap from the hedge bottoms

	Taxon	Mature hedges			New hedges			Hedgeless boundaries		
		April	July	Sept	April	July	Sept	April	July	Sept
		n = 16	n = 16	n = 16	n = 16	n = 16	n = 15	n = 4	n = 4	n = 4
1	**Acari**	1,541	3,276	757	1,158	3,544	635	186	799	284
2	**Araneae**	143	349	134	305	242	150	222	107	56
3	**Coleoptera**	580	591	329	306	448	270	77	136	89
4	**Collembola**	4,037	1,491	731	4,969	2,699	754	443	831	431
5	**Dermaptera**	30	250	8	30	63	4	0	2	1
6	**Diptera**	638	836	1,040	395	654	741	105	236	260
7	**Geophilomorpha**	1	0	0	0	0	0	0	0	0
8	**Hemiptera**	669	1,641	376	301	1,080	594	142	626	454
9	**Hymenoptera**	339	2,034	825	2,412	5,496	1,064	55	441	273
10	**Isopoda**	32	181	108	19	82	66	4	17	10
11	**Julida**	11	16	71	4	8	11	3	0	1
12	**Lepidoptera**	16	23	11	21	46	8	3	4	5
13	**Mecoptera**	0	0	0	0	0	3	0	0	0
14	**Neuroptera**	1	1	0	0	0	0	0	0	0
15	**Opiliones**	174	472	660	101	612	573	33	129	285
16	**Orthoptera**	0	0	0	0	1	1	1	0	0
17	**Polydesmida**	2	2	14	1	1	1	0	0	0
18	**Pseudoscorpiones**	0	0	3	0	0	0	0	0	1
19	**Psocoptera**	3	14	31	1	7	15	0	0	0
20	**Pulmonata**	1	16	8	10	27	4	0	3	2
21	**Siphonaptera**	0	5	5	0	7	12	0	2	1
22	**Thysanoptera**	237	1,802	83	144	543	61	48	81	13
	TOTAL	**8,455**	**13,000**	**5,194**	**10,177**	**15,560**	**4,967**	**1,322**	**3,414**	**2,166**
	Frequencies:									
	No. of taxa	18	18	18	16	18	19	13	14	16
	Absent	4	4	4	6	4	3	9	8	6
	Singletons =1	3	1	0	2	2	2	1	0	4
	Doubletons =2	1	2	1	1	1	1	1	3	1

Table B2. Sticky trap abundances (Total, mean, ± SD, ± SE) by taxon and month – April

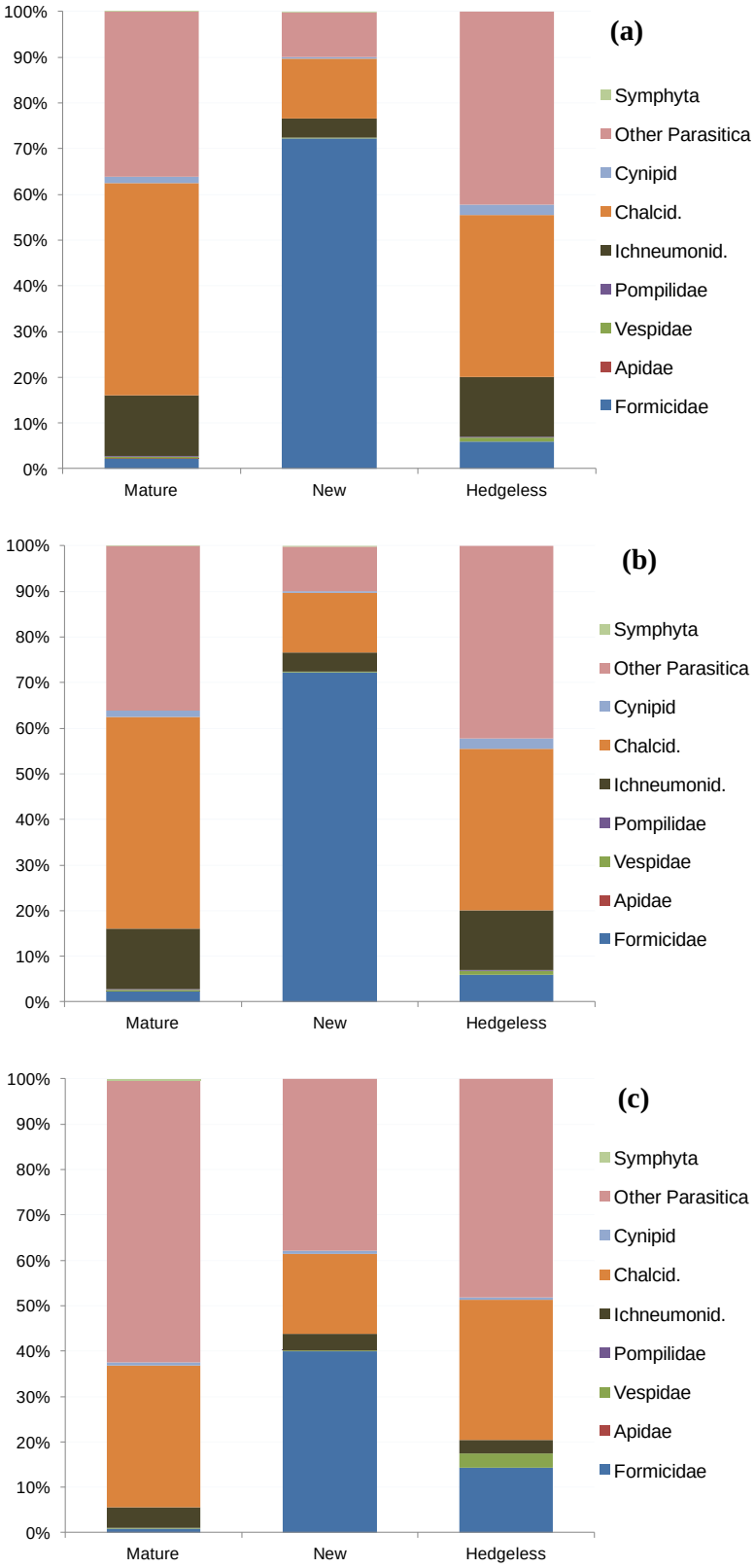
STICKY TRAPS	APRIL	Mature hedges (n = 16)			APRIL	New hedges (n = 16)			APRIL	Hedgeless (n = 4)		
Taxon	Total	Mean	+/- SD	+/- SE	Total	Mean	+/- SD	+/- SE	Total	Mean	+/- SD	+/- SE
Collembola	4037	252.31	191.42	47.86	4969	310.56	196.51	49.13	443	110.75	70.70	35.35
Acari	1541	96.31	95.44	23.86	1158	72.38	65.50	16.37	186	46.50	23.01	11.51
Hemiptera	669	41.81	77.43	19.36	301	18.81	24.39	6.10	142	35.50	57.81	28.91
Diptera	638	39.88	28.06	7.02	395	24.69	17.32	4.33	105	26.25	18.43	9.21
Coleoptera	580	36.25	32.04	8.01	306	19.13	10.86	2.71	77	19.25	20.39	10.19
Hymenoptera	339	21.19	23.97	5.99	2412	150.75	402.02	100.51	55	13.75	13.89	6.94
Thysanoptera	237	14.81	10.91	2.73	144	9.00	5.96	1.49	48	12.00	16.91	8.46
Opiliones	174	10.88	16.79	4.20	101	6.31	5.79	1.45	33	8.25	9.11	4.55
Araneae	143	8.94	7.20	1.80	305	19.06	11.86	2.96	222	55.50	46.72	23.36
Isopoda	32	2.00	2.25	0.56	19	1.19	1.38	0.34	4	1.00	0.82	0.41
Dermaptera	30	1.88	4.80	1.20	30	1.88	5.48	1.37	0	0.00	0.00	0.00
Lepidoptera	16	1.00	0.63	0.16	21	1.31	1.49	0.37	3	0.75	0.96	0.48
Julida	11	0.69	0.95	0.24	4	0.25	0.58	0.14	3	0.75	0.96	0.48
Psocoptera	3	0.19	0.40	0.10	1	0.06	0.25	0.06	0	0.00	0.00	0.00
Polydesmida	2	0.13	0.34	0.09	1	0.06	0.25	0.06	0	0.00	0.00	0.00
Geophilomorpha	1	0.06	0.25	0.06	0	0.00	0.00	0.00	0	0.00	0.00	0.00
Pulmonata	1	0.06	0.25	0.06	10	0.63	1.50	0.38	0	0.00	0.00	0.00
Neuroptera	1	0.06	0.25	0.06	0	0.00	0.00	0.00	0	0.00	0.00	0.00
Siphonaptera	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0	0.00	0.00	0.00
Orthoptera	0	0.00	0.00	0.00	0	0.00	0.00	0.00	1	0.25	0.50	0.25
Mecoptera	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0	0.00	0.00	0.00
Pseudoscorpiones	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0	0.00	0.00	0.00

Table B3. Sticky trap abundances (Total, mean, ± SD, ± SE) by taxon and month – July

STICKY TRAPS	JULY	Mature hedges (n = 16)			JULY	New hedges (n = 16)			JULY	Hedgeless (n = 4)		
Taxon	Total	Mean	+/- SD	+/- SE	Total	Mean	+/- SD	+/- SE	Total	Mean	+/- SD	+/- SE
Acari	3276	204.75	129.32	32.33	3544	221.50	113.26	28.31	799	199.75	100.73	50.37
Hymenoptera	2034	127.13	52.30	13.08	5496	343.50	904.04	226.01	441	110.25	13.82	6.91
Thysanoptera	1802	112.63	98.11	24.53	543	33.94	27.23	6.81	81	20.25	7.89	3.94
Hemiptera	1641	102.56	59.06	14.77	1080	67.50	44.88	11.22	626	156.50	141.71	70.85
Collembola	1491	93.19	49.54	12.38	2699	168.69	107.99	27.00	831	207.75	81.18	40.59
Diptera	836	52.25	30.52	7.63	654	40.88	26.28	6.57	236	59.00	13.29	6.65
Coleoptera	591	36.94	10.04	2.51	448	28.00	10.33	2.58	136	34.00	16.43	8.22
Opiliones	472	29.50	19.22	4.81	612	38.25	22.32	5.58	129	32.25	19.87	9.94
Araneae	349	21.81	8.92	2.23	242	15.13	5.50	1.38	107	26.75	4.11	2.06
Dermaptera	250	15.63	17.70	4.42	63	3.94	4.75	1.19	2	0.50	1.00	0.50
Isopoda	181	11.31	14.96	3.74	82	5.13	5.85	1.46	17	4.25	2.50	1.25
Lepidoptera	23	1.44	1.21	0.30	46	2.88	2.36	0.59	4	1.00	1.41	0.71
Julida	16	1.00	1.32	0.33	8	0.50	1.03	0.26	0	0.00	0.00	0.00
Pulmonata	16	1.00	2.22	0.56	27	1.69	2.39	0.60	3	0.75	1.50	0.75
Psocoptera	14	0.88	1.89	0.47	7	0.44	0.89	0.22	0	0.00	0.00	0.00
Siphonaptera	5	0.31	0.60	0.15	7	0.44	0.63	0.16	2	0.50	0.58	0.29
Polydesmida	2	0.13	0.34	0.09	1	0.06	0.25	0.06	0	0.00	0.00	0.00
Neuroptera	1	0.06	0.25	0.06	0	0.00	0.00	0.00	0	0.00	0.00	0.00
Geophilomorpha	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0	0.00	0.00	0.00
Orthoptera	0	0.00	0.00	0.00	1	0.06	0.25	0.06	0	0.00	0.00	0.00
Mecoptera	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0	0.00	0.00	0.00
Pseudoscorpiones	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0	0.00	0.00	0.00

Table B4. Sticky trap abundances (Total, mean, ± SD, ± SE) by taxon and month – September

STICKY TRAPS	SEPT	Mature hedges (n = 16)			SEPT	New hedges (n = 15)			SEPT	Hedgeless (n = 4)		
Taxon	Total	Mean	+/- SD	+/- SE	Total	Mean	+/- SD	+/- SE	Total	Mean	+/- SD	+/- SE
Diptera	1040	65.00	46.13	11.53	741	49.40	37.69	9.73	260	65.00	25.21	12.60
Hymenoptera	825	51.56	21.38	5.34	1064	70.93	95.62	24.69	273	68.25	3.77	1.89
Acari	757	47.31	30.85	7.71	635	42.33	31.42	8.11	284	71.00	58.38	29.19
Collembola	731	45.69	28.78	7.19	754	50.27	42.05	10.86	431	107.75	78.86	39.43
Opiliones	660	41.25	30.56	7.64	573	38.20	31.51	8.14	285	71.25	36.87	18.44
Hemiptera	376	23.50	15.50	3.88	594	39.60	24.47	6.32	454	113.50	147.81	73.90
Coleoptera	329	20.56	10.75	2.69	270	18.00	10.35	2.67	89	22.25	4.50	2.25
Araneae	134	8.38	3.12	0.78	150	10.00	4.60	1.19	56	14.00	5.77	2.89
Isopoda	108	6.75	10.35	2.59	66	4.40	8.41	2.17	10	2.50	3.32	1.66
Thysanoptera	83	5.19	3.53	0.88	61	4.07	2.28	0.59	13	3.25	1.89	0.95
Julida	71	4.44	13.09	3.27	11	0.73	1.22	0.32	1	0.25	0.50	0.25
Psocoptera	31	1.94	1.53	0.38	15	1.00	1.41	0.37	0	0.00	0.00	0.00
Polydesmida	14	0.88	1.50	0.38	1	0.07	0.26	0.07	0	0.00	0.00	0.00
Lepidoptera	11	0.69	1.01	0.25	8	0.53	0.52	0.13	5	1.25	0.96	0.48
Dermaptera	8	0.50	0.63	0.16	4	0.27	0.70	0.18	1	0.25	0.50	0.25
Pulmonata	8	0.50	1.26	0.32	4	0.27	0.59	0.15	2	0.50	0.58	0.29
Siphonaptera	5	0.31	0.48	0.12	12	0.80	0.77	0.20	1	0.25	0.50	0.25
Pseudoscorpiones	3	0.19	0.54	0.14	0	0.00	0.00	0.00	1	0.25	0.50	0.25
Geophilomorpha	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0	0.00	0.00	0.00
Orthoptera	0	0.00	0.00	0.00	1	0.07	0.26	0.07	0	0.00	0.00	0.00
Mecoptera	0	0.00	0.00	0.00	3	0.20	0.77	0.20	0	0.00	0.00	0.00
Neuroptera	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0	0.00	0.00	0.00



Figures B1 (a)–(c). Stacked column charts showing the proportional abundance of sub-classifications of Hymenoptera in Mature hedges (n = 16), New hedges (n = 16) and Hedgeless boundaries (n = 4) for: (a) April, (b) July and (c) September. Categories shown highlight differences between Formicidae and Parasitica (Ichneumonidoidea, Chalcidoidea, Cynipidae and Other Parasitica) and other groups

Table B5. Counts of families/superfamilies of Diptera found on sticky traps in Mature hedges, New hedges and Hedgeless boundaries, April 2011. Abundance and relative % of Dipteran assemblage shown

April		Mature hedges (n = 16)		New hedges (n = 16)		Hedgeless boundaries (n = 4)	
Suborder	Family/superfamily	Abundance	% of order	Abundance	% of order	Abundance	% of order
Brachycera	Agromyzidae	2	0	0	0	0	0
Brachycera	Anthomyiidae	0	0	3	1	0	0
Brachycera	Chloropidae	3	0	3	1	0	0
Brachycera	Dolichopopidae	0	0	0	0	0	0
Brachycera	Empididae	3	0	4	1	1	1
Brachycera	Hybotidae	2	0	1	0	0	0
Brachycera	Muscidae	5	1	1	0	3	3
Brachycera	Opomyzidae	1	0	1	0	0	0
Brachycera	Other Brachycera	28	4	24	6	17	16
Brachycera	Phoridae	66	10	44	11	17	16
Brachycera	Piophilidae	1	0	0	0	0	0
Brachycera	Psilidae	1	0	1	0	1	1
Brachycera	Sarcophagidae	0	0	0	0	1	1
Brachycera	Sciomyzidae	0	0	0	0	0	0
Brachycera	Syrphidae	0	0	0	0	0	0
Nematocera	Bibionidae	7	1	13	3	0	0
Nematocera	Cecidomyiidae	58	9	33	8	7	7
Nematocera	Chironomidae	4	1	1	0	0	0
Nematocera	Culicidae	4	1	0	0	0	0
Nematocera	Mycetophilidae	3	0	6	2	0	0
Nematocera	Other Nematocera	83	13	50	13	5	5
Nematocera	Psychodidae	10	2	12	3	0	0
Nematocera	Sciaridae	346	54	187	47	42	40
Nematocera	Tipulidae	0	0	0	0	1	1
Unidentified	Adult	8	1	9	2	6	6
Unidentified	Larval	3	0	2	1	4	4
	Total Diptera	**638**	**100%**	**395**	**100%**	**105**	**100%**

Table B6. Counts of families/superfamilies of Diptera found on sticky traps in Mature hedges, New hedges and Hedgeless boundaries, July 2011. Abundance and relative % of Dipteran assemblage shown

July		Mature hedges (n = 16)		New hedges (n = 16)		Hedgeless boundaries (n = 4)	
Suborder	Family/superfamily	Abundance	% of order	Abundance	% of order	Abundance	% of order
Brachycera	Agromyzidae	45	5	6	1	1	0
Brachycera	Anthomyzidae	5	1	1	0	0	0
Brachycera	Calliphoridae	4	0	0	0	2	1
Brachycera	Chloropidae	2	0	5	1	1	0
Brachycera	Dolichopopidae	22	3	36	6	8	3
Brachycera	Drosophilidae	0	0	2	0	0	0
Brachycera	Empididae	3	0	2	0	1	0
Brachycera	Ephydridae	7	1	7	1	4	2
Brachycera	Heleomyzidae	4	0	0	0	2	1
Brachycera	Hybotidae	3	0	2	0	1	0
Brachycera	Lonchopteridae	1	0	1	0	3	1
Brachycera	Lonchaeidae	0	0	2	0	1	0
Brachycera	Megamerinidae	1	0	0	0	0	0
Brachycera	Micropezidae	10	1	42	6	0	0
Brachycera	Muscidae	11	1	12	2	13	6
Brachycera	Opomyzidae	7	1	13	2	4	2
Brachycera	Phoridae	314	38	187	29	86	36
Brachycera	Sciomyzidae	2	0	2	0	0	0
Brachycera	Sepsidae	0	0	0	0	1	0
Brachycera	Sphaeroceridae	10	1	16	2	10	4
Brachycera	Syrphidae	3	0	2	0	1	0
Brachycera	Tachinidae	3	0	1	0	0	0
Brachycera	Therevidae	2	0	3	0	4	2
Brachycera	Other Brachycera	61	7	117	18	26	11
Nematocera	Cecidomyiidae	38	5	16	2	3	1
Nematocera	Mycetophilidae	2	0	0	0	0	0
Nematocera	Other Nematocera	103	12	54	8	13	6
Nematocera	Psychodidae	17	2	16	2	3	1
Nematocera	Scatopsidae	2	0	3	0	0	0
Nematocera	Sciaridae	110	13	55	8	16	7
Nematocera	Tipulidae	1	0	1	0	1	0
Unidentified	Adult	20	2	23	4	3	1
Unidentified	Larval	23	3	27	4	28	12
	Total Diptera	**836**	**100%**	**654**	**100%**	**236**	**100%**

Table B7. Families/superfamilies of Diptera found on sticky traps in Mature hedges, New hedges and Hedgeless boundaries, September 2011. Abundance and relative % of Dipteran assemblage shown

September		Mature hedges (n = 16)		New hedges (n = 15)		Hedgeless boundaries (n = 4)	
Suborder	Family/superfamily	Abundance	% of order	Abundance	% of order	Abundance	% of order
Brachycera	Anthomyzidae	3	0	2	0	2	1
Brachycera	Calliphoridae	3	0	1	0	6	2
Brachycera	Chloropidae	2	0	1	0	0	0
Brachycera	Dolichopopidae	46	4	13	2	0	0
Brachycera	Drosophilidae	1	0	0	0	0	0
Brachycera	Empididae	0	0	0	0	0	0
Brachycera	Ephydridae	3	0	5	1	1	0
Brachycera	Fanniidae	1	0	0	0	0	0
Brachycera	Longchopteridae	5	0	4	1	2	1
Brachycera	Micropezidae	3	0	0	0	0	0
Brachycera	Muscidae	39	4	35	5	13	5
Brachycera	Odiniidae	0	0	0	0	1	0
Brachycera	Opomyzidae	8	1	6	1	8	3
Brachycera	Other Brachycera	14	1	19	3	14	5
Brachycera	Pallopteridae	0	0	2	0	0	0
Brachycera	Phoridae	152	15	87	12	21	8
Brachycera	Sarcophagidae	1	0	1	0	0	0
Brachycera	Sciomyzidae	2	0	4	1	8	3
Brachycera	Sepsidae	1	0	0	0	0	0
Brachycera	Sphaeroceridae	7	1	4	1	1	0
Brachycera	Syrphidae	0	0	0	0	0	0
Brachycera	Therevidae	0	0	0	0	0	0
Nematocera	Cecidomyiidae	70	7	49	7	3	1
Nematocera	Culicidae	2	0	0	0	0	0
Nematocera	Mycetophilidae	1	0	0	0	0	0
Nematocera	Other Nematocera	218	21	116	16	23	9
Nematocera	Psychodidae	79	8	187	25	28	11
Nematocera	Scatopsidae	8	1	1	0	0	0
Nematocera	Sciaridae	332	32	165	22	88	34
Nematocera	Tipulidae	0	0	0	0	0	0
Unidentified	Adult	19	2	10	1	4	2
Unidentified	Larval	20	2	29	4	37	15
	Total Diptera	**1040**	**100%**	**741**	**100%**	**260**	**100%**

Table B8. Families/superfamilies of Coleoptera found on sticky traps in Mature hedges, New hedges and Hedgeless boundaries, April 2011. Abundance and relative % of Coleopteran assemblage shown

April	Mature hedges (n = 16)		New hedges (n = 16)		Hedgeless boundaries (n = 4)	
Family/superfamily	Abundance	% of Total	Abundance	% of Total	Abundance	% of Total
Anobiidae	1	0	0	0	0	0
Carabidae	76	13	95	31	25	32
Chrysomelidae	61	11	13	4	2	3
Cisidae	1	0	0	0	0	0
Coccinelidae	2	0	3	1	0	0
Cryptophagidae	88	15	23	8	3	4
Curculionoidea	15	3	36	12	34	44
Dascillidae	2	0	0	0	0	0
Dermestidae	1	0	0	0	0	0
Dytiscidae	2	0	0	0	0	0
Elateridae	3	1	2	1	1	1
Histeridae	0	0	1	0	0	0
Latridiidae	94	16	39	13	5	6
Leiodidae	34	6	7	2	0	0
Mycetophagidae	1	0	1	0	0	0
Nitidulidae	4	1	12	4	0	0
Phloiophilidae	5	1	0	0	0	0
Ptilidae	34	6	0	0	2	3
Salpingidae	2	0	0	0	0	0
Scaphidiidae	0	0	1	0	0	0
Scarabeidae	0	0	2	1	0	0
Scirtidae	7	1	2	1	2	3
Staphylinidae	105	18	62	20	3	4
Adult (unidentified)	28	5	3	1	0	0
Larval (unidentified)	14	2	4	1	3	4
Total Coleoptera	**580**	**100%**	**306**	**100%**	**77**	**100%**

Table B9. Families/superfamilies of Coleoptera found on sticky traps in Mature hedges, New hedges and Hedgeless boundaries, July 2011. Abundance and relative % of Coleopteran assemblage shown

July	Mature hedges (n = 16)		New hedges (n = 16)		Hedgeless boundaries (n = 4)	
Family/superfamily	Abundance	% of Total	Abundance	% of Total	Abundance	% of Total
Anobiidae	3	1	0	0	0	0
Cantharidae	1	0	2	0	0	0
Carabidae	101	17	86	19	21	15
Chrysomelidae	10	2	16	4	13	10
Cisidae	5	1	2	0	1	1
Coccinelidae	2	0	3	1	1	1
Corylophidae	1	0	0	0	0	0
Cryptophagidae	88	15	63	14	10	7
Curculionoidea	28	5	52	12	8	6
Elateridae	0	0	1	0	17	13
Hydrophilidae	0	0	2	0	0	0
Latridiidae	58	10	33	7	11	8
Leiodidae	0	0	1	0	0	0
Melandryidae	1	0	1	0	0	0
Melyridae	1	0	0	0	0	0
Monotomidae	1	0	0	0	0	0
Mycetophagidae	2	0	1	0	0	0
Nitidulidae	3	1	3	1	2	1
Ptilidae	19	3	4	1	1	1
Ptinidae	0	0	1	0	0	0
Salpingidae	2	0	2	0	0	0
Sphindidae	1	0	0	0	0	0
Staphylinidae	202	34	147	33	47	35
Adult (unidentified)	30	5	4	1	0	0
Larval (unidentified)	32	5	24	5	4	3
Total Coleoptera	**591**	**100%**	**448**	**100%**	**136**	**100%**

Table B10. Families/superfamilies of Coleoptera found on sticky traps in Mature hedges, New hedges and Hedgeless boundaries, September 2011. Abundance and relative % of Coleopteran assemblage shown

September	Mature hedges (n = 16)		New hedges (n = 15)		Hedgeless boundaries (n = 4)	
Family/superfamily	Abundance	% of Total	Abundance	% of Total	Abundance	% of Total
Aderidae	1	0	0	0	0	0
Carabidae	65	20	40	15	41	46
Chrysomelidae	22	7	17	6	4	4
Coccinellidae	1	0	5	2	2	2
Cryptophagidae	17	5	7	3	4	4
Curculionoidea	11	3	9	3	3	3
Eucetinidae	16	5	5	2	0	0
Latridiidae	52	16	33	12	5	6
Leiodidae	0	0	1	0	0	0
Melyridae (Cleroidea)	1	0	0	0	0	0
Nitidulidae	0	0	1	0	0	0
Phalacridae	1	0	0	0	0	0
Ptilidae	9	3	0	0	1	1
Scydmaenidae	0	0	2	1	0	0
Staphylinidae	94	29	92	34	23	26
Larval (unidentified)	39	12	58	21	6	7
Total Coleoptera	**329**	**100%**	**270**	**100%**	**89**	**100%**

Table B11. Mean total abundance (± SD & ± SE) of all invertebrates and all taxa for each boundary type (Mature hedge, New hedge, Hedgeless boundary) and month (April, July, September) 2011

Boundary type	Month	Mean.	± SD	± SE
Mature hedge	April	528.44	315.03	78.76
	July	812.5	243.38	60.84
	Sept	324.63	87.5	21.87
New hedge	April	636.06	422.54	105.64
	July	972.5	828.72	207.18
	Sept	331.13	143.96	37.17
Hedgeless boundary	April	330.5	202.49	101.24
	July	853.5	250.13	125.06
	Sept	541.5	302.92	151.46

Table B12. Results of Spearman's *rho* correlations between hedgerow age (years) and abundance of invertebrate taxa at ground level (both in total and for each individual taxon) for all months combined and individually (April, July, September) for Mature and New hedges combined (n=32). Values are r_s plus significance values. Significant values are highlighted in bold. A Benjamini –Yekultieli method FDR corrected significance level of 0.014 applies

Taxon	All months		April		July		September	
	r_s	*p*	r_s	*p*	r_s	*p*	r_s	*p*
All taxa – total	0.216	0.236	0.124	0.499	0.193	0.290	0.053	0.776
Acari	0.157	0.391	0.253	0.162	0.122	0.505	0.077	0.682
Araneae	-0.063	0.733	-0.248	0.171	0.180	0.325	-0.180	0.334
Coleoptera	**0.549**	**0.001**	0.267	0.140	**0.613**	**<0.001**	0.253	0.170
Collembola	0.031	0.865	0.176	0.335	-0.316	0.078	0.004	0.985
Dermaptera	0.227	0.212	-0.145	0.428	0.271	0.133	0.239	0.195
Diptera	**0.439**	**0.012**	0.382	0.031	0.344	0.054	0.339	0.062
Hemiptera	0.072	0.695	-0.030	0.871	0.299	0.096	-0.353	0.052
Hymenoptera	0.162	0.376	0.148	0.418	0.154	0.401	0.036	0.849
Isopoda	0.341	0.057	0.118	0.520	0.329	0.066	0.290	0.114
Julida	0.229	0.207	0.210	0.249	0.168	0.359	0.129	0.489
Lepidoptera	-0.345	0.053	0.062	0.737	-0.407	0.021	-0.106	0.572
Opiliones	-0.088	0.632	-0.031	0.868	-0.124	0.499	-0.089	0.635
Psocoptera	**0.462**	**0.008**	0.255	0.159	0.303	0.092	0.365	0.044
Pulmonata	-0.239	0.189	-0.382	0.031	-0.154	0.401	-0.179	0.337
Thysanoptera	**0.674**	**<0.001**	0.388	0.028	**0.661**	**<0.001**	0.167	0.371

Table B13. Results of Spearman's *rho* correlations between hedgerow age (years) and abundance of invertebrate taxa at ground level (both in total and for each individual taxon) for all months combined and individually (April, July, September) for the sub-set of New hedges only (n = 16*). Values are r_s plus significance values. Significant values are highlighted in bold. An FDR (Benjamini and Yekultieli) corrected significance level of 0.014 applies

Taxon	All months		April		July		September*	
	r_s	*p*	r_s	*p*	r_s	*p*	r_s	*p*
All taxa – total	0.358	0.173	0.512	0.043	0.257	0.337	-0.165	0.557
Acari	0.451	0.080	0.149	0.582	0.527	0.036	-0.075	0.790
Araneae	0.387	0.138	0.517	0.040	-0.295	0.267	0.084	0.767
Coleoptera	0.319	0.228	0.045	0.869	**0.627**	**0.009**	0.253	0.363
Collembola	0.577	0.019	**0.670**	**0.005**	0.158	0.559	-0.103	0.716
Dermaptera	-0.266	0.319	-0.366	0.163	-0.019	0.946	-0.442	0.099
Diptera	-0.207	0.442	-0.011	0.969	-0.070	0.797	-0.170	0.544
Hemiptera	-0.409	0.115	**-0.646**	**0.007**	-0.342	0.195	0.023	0.935
Hymenoptera	0.105	0.699	0.373	0.154	-0.071	0.793	-0.307	0.266
Isopoda	-0.004	0.989	-0.055	0.839	0.007	0.980	0.033	0.908
Julida	-0.242	0.367	-0.261	0.329	0.001	0.997	-0.196	0.483
Lepidoptera	-0.198	0.462	0.152	0.574	-0.171	0.527	-0.460	0.085
Opiliones	-0.290	0.277	0.200	0.457	-0.025	0.927	-0.483	0.068
Psocoptera	0.125	0.645	0.116	0.670	0.501	0.048	-0.111	0.694
Pulmonata	0.139	0.607	-0.131	0.630	0.214	0.427	-0.414	0.125
Thysanoptera	0.410	0.115	-0.013	0.962	0.522	0.038	0.219	0.432

* In September, n = 15 as one hedgerow was removed due to building works

Table B14. Spearman's *rho* correlations between abundance of individual taxa sticky trapped at ground level – all months combined and all boundaries (n = 107)

Taxa	Acari		Araneae		Coleoptera		Collembola		Dermaptera		Diptera		Hemiptera		Hymenoptera (all)		Hymenoptera (Parasitica)	
	r_s	p	r_s	p	r_s	p	r_s	p	r_s	p	r_s	p	r_s	p	r_s	p	r_s	p
Acari	1.000	.	**0.356**	**0.000**	**0.541**	**<0.001**	**0.305**	**0.001**	**0.290**	**0.002**	0.139	0.154	**0.327**	**0.001**	**0.473**	**<0.001**	**0.526**	**<0.001**
Araneae	**0.356**	**0.001**	1.000	.	**0.260**	**0.007**	**0.334**	**0.001**	**0.268**	**0.005**	0.004	0.971	**0.315**	**0.001**	**0.326**	**0.001**	0.247	0.010
Coleoptera	**0.541**	**<0.001**	**0.260**	**0.007**	1.000	.	0.144	0.138	0.199	0.040	**0.372**	**<0.001**	0.140	0.152	**0.465**	**<0.001**	**0.454**	**<0.001**
Collembola	**0.305**	**0.001**	**0.334**	**<0.001**	0.144	0.138	1.000	.	-0.037	0.704	-0.107	0.272	-0.055	0.575	-0.052	0.597	-0.155	0.110
Dermaptera	**0.290**	**0.002**	**0.268**	**0.005**	0.199	0.040	-0.037	0.704	1.000	.	0.103	0.289	**0.394**	**<0.001**	**0.392**	**<0.001**	**0.433**	**<0.001**
Diptera	0.139	0.154	0.004	0.971	**0.372**	**<0.001**	-0.107	0.272	0.103	0.289	1.000	.	0.194	0.046	**0.366**	**<0.001**	**0.460**	**<0.001**
Hemiptera	**0.327**	**0.001**	**0.315**	**0.001**	0.140	0.152	-0.055	0.575	**0.394**	**<0.001**	0.194	0.046	1.000		**0.428**	**<0.001**	**0.560**	**<0.001**
Hymenoptera (all)	**0.473**	**<0.001**	**0.326**	**0.001**	**0.465**	**<0.001**	-0.052	0.597	**0.392**	**<0.001**	**0.366**	**<0.001**	**0.428**	**<0.001**	1.000	.		
Hymenoptera (Parasitica)	**0.526**	**<0.001**	0.247	0.010	**0.454**	**<0.001**	-0.155	0.110	**0.433**	**<0.001**	**0.460**	**<0.001**	**0.560**	**<0.001**			1.00	
Isopoda	0.154	0.114	0.047	0.633	0.211	0.029	-0.026	0.793	**0.292**	**0.002**	**0.264**	**0.006**	**0.360**	**<0.001**	**0.471**	**<0.001**	**0.450**	**<0.001**
Julida	-0.081	0.410	-0.138	0.155	0.040	0.685	-0.202	0.037	0.075	0.445	0.092	0.346	-0.012	0.900	0.005	0.957	0.051	0.600
Lepidoptera	**0.275**	**0.004**	0.126	0.197	0.048	0.622	0.113	0.245	0.154	0.112	0.025	0.797	0.071	0.465	0.246	0.011	0.201	0.038
Opiliones	0.195	0.044	0.037	0.706	0.162	0.096	-0.250	0.010	0.120	0.218	0.192	0.048	**0.269**	**0.005**	**0.414**	**<0.001**	**0.435**	**<0.001**
Psocoptera	-0.239	0.013	-0.191	0.048	-0.001	0.995	-0.226	0.019	0.027	0.786	0.200	0.039	-0.027	0.782	0.063	0.522	0.138	0.156
Pulmonata	**0.290**	**0.002**	0.148	0.128	0.091	0.351	-0.056	0.564	0.223	0.021	-0.046	0.636	0.202	0.037	**0.365**	**<0.001**	0.230	0.017
Thysanoptera	**0.646**	**<0.001**	**0.319**	**0.001**	**0.466**	**<0.001**	**0.333**	**<0.001**	**0.396**	**<0.001**	0.105	0.280	**0.463**	**<0.001**	**0.380**	**<0.001**	**0.477**	**<0.001**

Cont'd overleaf

Table B14. cont'd

All months	Isopoda		Julida		Lepidoptera		Opiliones		Psocoptera		Pulmonata		Thysanoptera	
	r_s	p	r_s	p	r_s	p	r_s	p	r_s	p	r_s	p	r_s	p
Acari	0.154	0.114	-0.081	0.410	**0.275**	**0.004**	0.195	0.044	-0.239	0.013	**0.290**	**0.002**	**0.646**	**<0.001**
Araneae	0.047	0.633	-0.138	0.155	0.126	0.197	0.037	0.706	-0.191	0.048	0.148	0.128	**0.319**	**0.001**
Coleoptera	0.211	0.029	0.040	0.685	0.048	0.622	0.162	0.096	-0.001	0.995	0.091	0.351	**0.466**	**<0.001**
Collembola	-0.026	0.793	-0.202	0.037	0.113	0.245	-0.250	0.010	-0.226	0.019	-0.056	0.564	**0.333**	**<0.001**
Dermaptera	**0.292**	**0.002**	0.075	0.445	0.154	0.112	0.120	0.218	0.027	0.786	0.223	0.021	**0.396**	**<0.001**
Diptera	**0.264**	**0.006**	0.092	0.346	0.025	0.797	0.192	0.048	0.200	0.039	-0.046	0.636	0.105	0.280
Hemiptera	**0.360**	**<0.001**	-0.012	0.900	0.071	0.465	**0.269**	**0.005**	-0.027	0.782	0.202	0.037	**0.463**	**<0.001**
Hymenoptera (all)	**0.471**	**<0.001**	0.005	0.957	0.246	0.011	**0.414**	**<0.001**	0.063	0.522	**0.365**	**<0.001**	**0.380**	**<0.001**
Hymenoptera (Parasitica)	**0.450**	**<0.001**	0.051	0.600	0.201	0.038	**0.435**	**<0.001**	0.138	0.156	0.230	0.017	**0.477**	**<0.001**
Isopoda	1.000	.	0.198	0.041	-0.116	0.233	**0.391**	**<0.001**	0.209	0.031	0.101	0.300	0.232	0.016
Julida	0.198	0.041	1.000	.	-0.065	0.505	0.109	0.265	-0.104	0.286	-0.020	0.839	-0.030	0.759
Lepidoptera	-0.116	0.233	-0.065	0.505	1.000	.	-0.015	0.878	-0.150	0.122	0.157	0.106	0.222	0.022
Opiliones	**0.391**	**<0.001**	0.109	0.265	-0.015	0.878	1.000	.	0.167	0.086	0.254	0.008	-0.015	0.879
Psocoptera	0.209	0.031	-0.104	0.286	-0.150	0.122	0.167	0.086	1.000	.	-0.062	0.529	-0.115	0.237
Pulmonata	0.101	0.300	-0.020	0.839	0.157	0.106	**0.254**	**0.008**	-0.062	0.529	1.000	.	0.105	0.282
Thysanoptera	0.232	0.016	-0.030	0.759	0.222	0.022	-0.015	0.879	-0.115	0.237	0.105	0.282	1.000	.

Table B15. Spearman's *rho* correlations between the abundance of individual invertebrate taxa sticky trapped in the hedge bottom – all taxa – all months combined – hedges only (n = 95)

All months	Acari		Araneae		Coleoptera		Collembola		Dermaptera		Diptera		Hemiptera		Hymenoptera (all)		Hymenoptera (Parasitica)	
	r_s	*p*	r_s	*p*	r_s	*p*	r_s	*p*	r_s	*p*	r_s	*p*	r_s	*p*	r_s	*p*	r_s	*p*
Acari			**0.371**	**<0.001**	**0.519**	**<0.001**	**0.280**	**0.006**	**0.336**	**0.001**	0.095	0.360	**0.314**	**0.002**	**0.439**	**<0.001**	**0.494**	**<0.001**
Araneae	**0.371**	**<0.001**			0.260	0.011	**0.318**	**0.002**	**0.380**	**<0.001**	-0.036	0.728	**0.303**	**0.003**	**0.361**	**<0.001**	**0.262**	**0.010**
Coleoptera	**0.519**	**<0.001**	0.260	0.011			0.121	0.242	0.227	0.027	**0.339**	**0.001**	0.126	0.222	**0.441**	**<0.001**	**0.429**	**<0.001**
Collembola	**0.280**	**0.006**	**0.318**	**0.002**	0.121	0.242			-0.018	0.865	-0.173	0.094	-0.148	0.152	-0.099	0.339	-0.221	0.031
Dermaptera	**0.336**	**0.001**	**0.380**	**<0.001**	0.227	0.027	-0.018	0.865			0.110	0.289	**0.458**	**<0.001**	**0.405**	**<0.001**	**0.467**	**<0.001**
Diptera	0.095	0.360	-0.036	0.728	**0.339**	**0.001**	-0.173	0.094	0.110	0.289			0.119	0.249	**0.319**	**0.002**	**0.432**	**<0.001**
Hemiptera	**0.314**	**0.002**	**0.303**	**0.003**	0.126	0.222	-0.148	0.152	**0.458**	**<0.001**	0.119	0.249			**0.400**	**<0.001**	**0.551**	**<0.001**
Hymenoptera (all)	**0.439**	**<0.001**	**0.361**	**<0.001**	**0.441**	**<0.001**	-0.099	0.339	**0.405**	**<0.001**	**0.319**	**0.002**	**0.400**	**<0.001**				
Hymenoptera (Parasitica)	**0.494**	**<0.001**	0.262	0.010	**0.429**	**<0.001**	-0.221	0.031	**0.467**	**<0.001**	**0.432**	**<0.001**	**0.551**	**<0.001**				
Isopoda	0.121	0.244	0.062	0.549	0.198	0.055	-0.070	0.500	**0.284**	**0.005**	0.236	0.021	**0.310**	**0.002**	**0.475**	**<0.001**	**0.447**	**<0.001**
Julida	-0.061	0.557	-0.134	0.195	0.061	0.56	-0.21	0.041	0.074	0.476	0.150	0.147	0.021	0.843	0.042	0.683	0.091	0.379
Lepidoptera	**0.357**	**<0.001**	0.218	0.034	0.100	0.334	0.165	0.109	0.127	0.218	0.061	0.559	0.174	0.092	**0.275**	**0.007**	0.237	0.021
Opiliones	0.188	0.068	0.055	0.599	0.163	0.114	**-0.305**	**0.003**	0.140	0.177	0.108	0.300	0.268	0.009	**0.399**	**<0.001**	**0.422**	**<0.001**
Psocoptera	-0.248	0.015	-0.135	0.193	-0.002	0.987	-0.220	0.032	-0.019	0.857	0.240	0.019	-0.002	0.982	0.076	0.461	0.167	0.106
Pulmonata	**0.296**	**0.004**	0.207	0.044	0.080	0.440	-0.059	0.569	0.253	0.013	-0.068	0.514	**0.279**	**0.006**	**0.378**	**<0.001**	0.228	0.026
Thysanoptera	**0.672**	**<0.001**	**0.355**	**<0.001**	**0.498**	**<0.001**	**0.309**	**0.002**	**0.418**	**<0.001**	0.113	0.277	**0.451**	**<0.001**	**0.376**	**<0.001**	**0.479**	**<0.001**

Cont'd overleaf

Table B15. cont'd

All months	Isopoda		Julida		Lepidoptera		Opiliones		Psocoptera		Pulmonata		Thysanoptera	
	r_s	p	r_s	p	r_s	p	r_s	p	r_s	p	r_s	p	r_s	p
Acari	0.121	0.244	-0.061	0.557	**0.357**	**<0.001**	0.188	0.068	-0.248	0.015	**0.296**	**0.004**	**0.672**	**<0.001**
Araneae	0.062	0.549	-0.134	0.195	0.218	0.034	0.055	0.599	-0.135	0.193	0.207	0.044	**0.355**	**<0.001**
Coleoptera	0.198	0.055	0.061	0.560	0.100	0.334	0.163	0.114	-0.002	0.987	0.080	0.440	**0.498**	**<0.001**
Collembola	-0.070	0.500	-0.210	0.041	0.165	0.109	**-0.305**	**0.003**	-0.220	0.032	-0.059	0.569	**0.309**	**0.002**
Dermaptera	**0.284**	**0.005**	0.074	0.476	0.127	0.218	0.140	0.177	-0.019	0.857	0.253	0.013	**0.418**	**<0.001**
Diptera	0.236	0.021	0.150	0.147	0.061	0.559	0.108	0.300	0.240	0.019	-0.068	0.514	0.113	0.277
Hemiptera	**0.310**	**0.002**	0.021	0.843	0.174	0.092	0.268	0.009	-0.002	0.982	**0.279**	**0.006**	**0.451**	**<0.001**
Hymenoptera (all)	**0.475**	**<0.001**	0.042	0.683	**0.275**	**0.007**	**0.399**	**<0.001**	0.076	0.461	**0.378**	**<0.001**	**0.376**	**<0.001**
Hymenoptera (Parasitica)	**0.447**	**<0.001**	0.091	0.379	0.237	0.021	**0.422**	**<0.001**	0.167	0.106	0.228	0.026	**0.479**	**<0.001**
Isopoda			0.235	0.022	-0.089	0.390	**0.430**	**<0.001**	0.206	0.046	0.122	0.239	0.193	0.061
Julida	0.235	0.022			-0.053	0.610	0.176	0.088	-0.135	0.192	-0.027	0.791	-0.062	0.551
Lepidoptera	-0.089	0.390	-0.053	0.610			-0.055	0.596	-0.181	0.080	0.123	0.234	**0.297**	**0.004**
Opiliones	**0.430**	**<0.001**	0.176	0.088	-0.055	0.596			0.210	0.041	0.233	0.023	0.016	0.874
Psocoptera	0.206	0.046	-0.135	0.192	-0.181	0.080	0.210	0.041			-0.077	0.457	-0.156	0.131
Pulmonata	0.122	0.239	-0.027	0.791	0.123	0.234	0.233	0.023	-0.077	0.457			0.128	0.218
Thysanoptera	0.193	0.061	-0.062	0.551	**0.297**	**0.004**	0.016	0.874	-0.156	0.131	0.128	0.218		

Table B16. Spearman's *rho* correlations between abundance of individual taxa – Sticky traps – all boundaries (n = 36), April 2011

Taxa		Acari	Araneae	Coleoptera	Collembola	Dermaptera	Diptera	Hemiptera	Hymenoptera	Isopoda	Julida	Lepidoptera	Opiliones	Psocoptera	Pulmonata	Thysanoptera
Acari	r_s		0.135	**0.474**	**0.435**	0.074	0.277	-0.037	0.337	-0.019	-0.146	-0.004	0.051	-0.072	-0.084	0.382
	p		0.432	**0.003**	**0.008**	0.669	0.102	0.832	0.044	0.911	0.397	0.980	0.766	0.675	0.628	0.022
Araneae	r_s	0.135		0.071	0.250	0.078	0.046	0.013	**0.461**	-0.080	-0.071	-0.082	-0.067	-0.060	0.223	-0.008
	p	0.432		0.680	0.141	0.650	0.788	0.939	**0.005**	0.642	0.681	0.633	0.696	0.730	0.191	0.963
Coleoptera	r_s	**0.474**	0.071		0.169	0.049	0.408	-0.119	**0.507**	-0.185	-0.239	0.016	0.043	-0.068	0.028	0.276
	p	**0.003**	0.680		0.325	0.775	0.014	0.491	**0.002**	0.280	0.160	0.927	0.804	0.693	0.873	0.103
Collembola	r_s	0.435	0.250	0.169		-0.196	0.143	-0.073	0.366	0.093	-0.238	0.043	0.123	0.281	0.101	0.418
	p	0.008	0.141	0.325		0.252	0.405	0.672	0.028	0.591	0.163	0.802	0.474	0.097	0.559	0.011
Dermaptera	r_s	0.074	0.078	0.049	-0.196		0.274	0.167	0.138	0.054	0.028	-0.191	-0.361	-0.202	0.282	0.060
	p	0.669	0.650	0.775	0.252		0.105	0.330	0.422	0.752	0.873	0.263	0.030	0.238	0.095	0.727
Diptera	r_s	0.277	0.046	0.408	0.143	0.274		0.243	**0.462**	-0.086	-0.030	0.161	-0.260	0.192	-0.195	**0.501**
	p	0.102	0.788	0.014	0.405	0.105		0.154	**0.005**	0.619	0.863	0.349	0.126	0.263	0.254	**0.002**
Hemiptera	r_s	-0.037	0.013	-0.119	-0.073	0.167	0.243		-0.039	0.238	0.242	-0.298	-0.310	-0.094	0.072	0.305
	p	0.832	0.939	0.491	0.672	0.330	0.154		0.820	0.162	0.154	0.078	0.066	0.586	0.677	0.071
Hymenoptera	r_s	0.337	**0.461**	**0.507**	0.366	0.138	**0.462**	-0.039		0.011	-0.009	0.122	-0.031	-0.141	0.189	0.286
	p	0.044	**0.005**	**0.002**	0.028	0.422	**0.005**	0.820		0.951	0.959	0.479	0.856	0.414	0.270	0.090
Isopoda	r_s	-0.019	-0.080	-0.185	0.093	0.054	-0.086	0.238	0.011		0.322	0.045	0.128	-0.044	0.156	-0.096
	p	0.911	0.642	0.280	0.591	0.752	0.619	0.162	0.951		0.055	0.794	0.456	0.797	0.364	0.579
Julida	r_s	-0.146	-0.071	-0.239	-0.238	0.028	-0.030	0.242	-0.009	0.322		-0.225	-0.107	-0.087	-0.309	0.085
	p	0.397	0.681	0.160	0.163	0.873	0.863	0.154	0.959	0.055		0.188	0.535	0.615	0.067	0.623
Lepidoptera	r_s	-0.004	-0.082	0.016	0.043	-0.191	0.161	-0.298	0.122	0.045	-0.225		-0.081	0.212	0.017	-0.166
	p	0.980	0.633	0.927	0.802	0.263	0.349	0.078	0.479	0.794	0.188		0.637	0.214	0.920	0.333
Opiliones	r_s	0.051	-0.067	0.043	0.123	-0.361	-0.260	-0.310	-0.031	0.128	-0.107	-0.081		0.026	0.242	-0.059
	p	0.766	0.696	0.804	0.474	0.030	0.126	0.066	0.856	0.456	0.535	0.637		0.882	0.155	0.734
Psocoptera	r_s	-0.072	-0.060	-0.068	0.281	-0.202	0.192	-0.094	-0.141	-0.044	-0.087	0.212	0.026		-0.158	0.094
	p	0.675	0.730	0.693	0.097	0.238	0.263	0.586	0.414	0.797	0.615	0.214	0.882		0.358	0.586
Pulmonata	r_s	-0.084	0.223	0.028	0.101	0.282	-0.195	0.072	0.189	0.156	-0.309	0.017	0.242	-0.158		-0.201
	p	0.628	0.191	0.873	0.559	0.095	0.254	0.677	0.270	0.364	0.067	0.920	0.155	0.358		0.240
Thysanoptera	r_s	0.382	-0.008	0.276	0.418	0.060	**0.501**	0.305	0.286	-0.096	0.085	-0.166	-0.059	0.094	-0.201	
	p	0.022	0.963	0.103	0.011	0.727	**0.002**	0.071	0.090	0.579	0.623	0.333	0.734	0.586	0.240	

The abundances of the following taxa were removed due to low abundance/overdispersion: Geophilomorpha, Polydesmida, Mecoptera, Neuroptera, Siphonaptera.

Table B17. Spearman's rho correlations between abundance of individual taxa – Sticky traps – all boundary types (n = 36), July 2011

Taxa		Acari	Araneae	Coleoptera	Collembola	Dermaptera	Diptera	Hemiptera	Hymenoptera	Isopoda	Julida	Lepidoptera	Opiliones	Psocoptera	Pulmonata	Thysanoptera
Acari	r_s		0.009	0.138	0.106	-0.064	0.052	-0.151	0.179	-0.057	0.159	-0.153	0.311	-0.056	0.422*	0.137
	p		0.956	0.421	0.540	0.709	0.765	0.381	0.297	0.74	0.356	0.374	0.065	0.744	0.01	0.424
Araneae	r_s	0.009		0.278	0.237	0.084	0.218	0.367*	-0.172	-0.101	0.144	-0.188	0.325	-0.044	-0.047	-0.197
	p	0.956		0.100	0.164	0.626	0.201	0.028	0.316	0.557	0.400	0.273	0.053	0.8	0.784	0.251
Coleoptera	r_s	0.138	0.278		-0.025	-0.032	0.311	0.214	-0.024	0.179	0.269	-0.264	-0.107	0.246	-0.104	0.441**
	p	0.421	0.100		0.883	0.852	0.065	0.210	0.888	0.296	0.112	0.119	0.533	0.149	0.544	0.007
Collembola	r_s	0.106	0.237	-0.025		-0.319	-0.003	-0.085	-0.287	-0.029	-0.342*	0.028	0.243	0	-0.106	-0.159
	p	0.54	0.164	0.883		0.058	0.985	0.624	0.089	0.869	0.041	0.87	0.153	0.999	0.537	0.354
Dermaptera	r_s	-0.064	0.084	-0.032	-0.319		-0.156	0.169	0.004	0.24	0.064	-0.011	0.301		0.053	0.05
	p	0.709	0.626	0.852	0.058		0.364	0.325	0.982	0.158	0.71	0.948	0.074		0.76	0.774
Diptera	r_s	0.052	0.218	0.311	-0.003	-0.156		0.175	0.235	0.161	-0.026	0.002	-0.074	0.095	-0.110	0.239
	p	0.765	0.201	0.065	0.985	0.364		0.308	0.167	0.348	0.879	0.992	0.667	0.582	0.521	0.161
Hemiptera	r_s	-0.151	0.367*	0.214	-0.085	0.169	0.175		0.331*	0.068	-0.068	-0.038	-0.004	-0.001	-0.207	0.125
	p	0.381	0.028	0.210	0.624	0.325	0.308		0.049	0.693	0.693	0.824	0.983	0.995	0.226	0.469
Hymenoptera	r_s	0.179	-0.172	-0.024	-0.287	0.004	0.235	0.331*		0.296	-0.037	-0.023	0.018	0.202	0.183	**0.461****
	p	0.297	0.316	0.888	0.089	0.982	0.167	0.049		0.079	0.83	0.895	0.917	0.237	0.286	**0.005**
Isopoda	r_s	-0.057	-0.101	0.179	-0.029	0.24	0.161	0.068	0.296		-0.004	-0.445**	0.238	0.052	-0.029	0.345*
	p	0.740	0.557	0.296	0.869	0.158	0.348	0.693	0.079		0.981	0.007	0.162	0.762	0.867	0.040
Julida	r_s	0.159	0.144	0.269	-0.342*	0.064	-0.026	-0.068	-0.037	-0.004		0.053	0.025	-0.338*	-0.084	0.099
	p	0.356	0.400	0.112	0.041	0.710	0.879	0.693	0.830	0.981		0.760	0.884	0.044	0.628	0.564
Lepidoptera	r_s	-0.153	-0.188	-0.264	0.028	-0.011	0.002	-0.038	-0.023	-0.445**	0.053		-0.108	0.079	-0.026	-0.138
	p	0.374	0.273	0.119	0.870	0.948	0.992	0.824	0.895	0.007	0.760		0.530	0.646	0.878	0.422
Opiliones	r_s	0.311	0.325	-0.107	0.243	0.301	-0.074	-0.004	0.018	0.238	0.025	-0.108		-0.204	0.062	-0.176
	p	0.065	0.053	0.533	0.153	0.074	0.667	0.983	0.917	0.162	0.884	0.530		0.233	0.721	0.304
Psocoptera	r_s	-0.056	-0.044	0.246	0	0.214	0.095	-0.001	0.202	0.052	-0.338*	0.079	-0.204		0.152	0.337*
	p	0.744	0.800	0.149	0.999	0.209	0.582	0.995	0.237	0.762	0.044	0.646	0.233		0.376	0.045
Pulmonata	r_s	0.422*	-0.047	-0.104	-0.106	0.053	-0.110	-0.207	0.183	-0.029	-0.084	-0.026	0.062	0.152		-0.084
	p	0.010	0.784	0.544	0.537	0.76	0.521	0.226	0.286	0.867	0.628	0.878	0.721	0.376		0.627
Thysanoptera	r_s	0.137	-0.197	0.441**	-0.159	0.050	0.239	0.125	0.461**	0.345*	0.099	-0.138	-0.176	0.337*	-0.084	
	p	0.424	0.251	0.007	0.354	0.774	0.161	0.469	0.005	0.040	0.564	0.422	0.304	0.045	0.627	

Table B18. Spearman's rho correlations between abundance of individual taxa – Sticky traps – all boundary types (n = 35), September 2011

Taxa		Acari	Araneae	Coleoptera	Collembola	Dermaptera	Diptera	Hemiptera	Hymenoptera	Isopoda	Julida	Lepidoptera	Opiliones	Psocoptera	Pulmonata	Thysanoptera
Acari	r_s		0.174	0.230	0.175	-0.202	0.066	0.038	0.190	-0.203	-0.081	0.166	0.418	-0.273	0.198	0.167
	p		0.317	0.184	0.316	0.245	0.706	0.829	0.274	0.242	0.646	0.341	0.013	0.112	0.253	0.338
Araneae	r_s	0.174		-0.039	0.181	-0.148	-0.171	0.306	-0.080	-0.047	-0.488	0.018	0.240	-0.020	-0.010	-0.136
	p	0.317		0.825	0.298	0.396	0.327	0.074	0.649	0.788	0.003	0.920	0.166	0.910	0.953	0.437
Coleoptera	r_s	0.230	-0.039		0.169	-0.114	**0.481**	-0.249	**0.520**	0.246	0.276	-0.303	0.336	0.205	-0.019	0.202
	p	0.184	0.825		0.332	0.515	**0.003**	0.149	**0.001**	0.154	0.108	0.077	0.048	0.237	0.916	0.245
Collembola	r_s	0.175	0.181	0.169		0.208	0.148	0.041	0.421	0.284	0.000	-0.204	0.139	-0.006	-0.096	-0.064
	p	0.316	0.298	0.332		0.231	0.397	0.815	0.012	0.098	0.999	0.240	0.426	0.973	0.582	0.714
Dermaptera	r_s	-0.202	-0.148	-0.114	0.208		0.138	0.003	0.047	0.110	0.124	-0.053	0.011	0.276	0.040	-0.096
	p	0.245	0.396	0.515	0.231		0.428	0.985	0.790	0.530	0.476	0.763	0.949	0.108	0.818	0.583
Diptera	r_s	0.066	-0.171	**0.481**	0.148	0.138		-0.144	**0.642**	0.349	0.269	-0.113	0.092	0.010	-0.111	-0.059
	p	0.706	0.327	**0.003**	0.397	0.428		0.409	**<0.001**	0.040	0.118	0.520	0.598	0.956	0.525	0.738
Hemiptera	r_s	0.038	0.306	-0.249	0.041	0.003	-0.144		-0.255	-0.044	-0.277	-0.093	0.213	-0.060	-0.041	0.076
	p	0.829	0.074	0.149	0.815	0.985	0.409		0.140	0.802	0.107	0.594	0.219	0.734	0.815	0.666
Hymenoptera	r_s	0.190	-0.080	**0.520**	0.421	0.047	**0.642**	-0.255		0.255	0.148	-0.091	0.276	0.078	-0.008	-0.243
	p	0.274	0.649	**0.001**	0.012	0.790	**<0.001**	0.140		0.139	0.395	0.604	0.109	0.656	0.962	0.160
Isopoda	r_s	-0.203	-0.047	0.246	0.284	0.110	0.349	-0.044	0.255		0.340	-0.299	0.153	0.302	-0.175	0.020
	p	0.242	0.788	0.154	0.098	0.530	0.040	0.802	0.139		0.046	0.081	0.380	0.078	0.315	0.909
Julida	r_s	-0.081	**-0.488**	0.276	0.000	0.124	0.269	-0.277	0.148	0.340		0.003	0.178	-0.136	0.279	0.073
	p	0.646	**0.003**	0.108	0.999	0.476	0.118	0.107	0.395	0.046		0.987	0.306	0.435	0.105	0.678
Lepidoptera	r_s	0.166	0.018	-0.303	-0.204	-0.053	-0.113	-0.093	-0.091	-0.299	0.003		0.189	-0.311	0.183	-0.234
	p	0.341	0.920	0.077	0.240	0.763	0.520	0.594	0.604	0.081	0.987		0.278	0.069	0.293	0.177
Opiliones	r_s	0.418	0.240	0.336	0.139	0.011	0.092	0.213	0.276	0.153	0.178	0.189		-0.086	0.505	0.018
	p	0.013	0.166	0.048	0.426	0.949	0.598	0.219	0.109	0.380	0.306	0.278		0.625	0.002	0.919
Psocoptera	r_s	-0.273	-0.020	0.205	-0.006	0.276	0.010	-0.060	0.078	0.302	-0.136	-0.311	-0.086		-0.298	0.233
	p	0.112	0.910	0.237	0.973	0.108	0.956	0.734	0.656	0.078	0.435	0.069	0.625		0.082	0.179
Pulmonata	r_s	0.198	-0.010	-0.019	-0.096	0.040	-0.111	-0.041	-0.008	-0.175	0.279	0.183	0.505	-0.298		-0.172
	p	0.253	0.953	0.916	0.582	0.818	0.525	0.815	0.962	0.315	0.105	0.293	0.002	0.082		0.323
Thysanoptera	r_s	0.167	-0.136	0.202	-0.064	-0.096	-0.059	0.076	-0.243	0.020	0.073	-0.234	0.018	0.233	-0.172	
	p	0.338	0.437	0.245	0.714	0.583	0.738	0.666	0.160	0.909	0.678	0.177	0.919	0.179	0.323	

Table B19. Taxonomic richness five number summary (median, maximum, minimum, first quartile, third quartile) and mean numbers (± SD & ± SE) of invertebrate groups collected from all boundary types (Mature hedges, New hedges and Hedgeless boundaries) during April, July and September 2011

Boundary type	n	Month	Total no. of taxa	Minimum	Median	Maximum	Interquartile range	Mean	± SD	± SE
Mature hedge	16	April	18	10.00	12.00	14.00	11.00 - 12.25	11.75	1.13	0.32
	16	July	18	12.00	13.00	15.00	12.00 - 14.00	13.36	1.01	0.29
	16	September	18	10.00	13.00	15.00	13.00 - 14.00	13.25	1.39	0.35
New hedge	16	April	16	8.00	11.00	13.00	10.75 - 12.00	11.00	1.26	0.37
	16	July	18	11.00	13.00	15.00	12.00 - 14.00	13.20	1.37	0.40
	15	September	19	10.00	12.00	14.00	11.50 - 13.00	12.20	1.26	0.33
Hedgeless	4	April	13	9.00	10.50	12.00	9.75 - 11.25	10.50	1.29	0.65
	4	July	14	10.00	11.50	13.00	10.75 - 12.25	11.50	1.29	0.65
	4	September	16	11.00	11.50	13.00	11.00 - 12.25	11.75	0.96	0.48

Table B20. Berger-Parker five number summary and mean numbers (± SD & ± SE) of invertebrate groups collected from all boundary types (Mature hedges, New hedges and Hedgeless boundaries) during April, July and September 2011

Boundary type	n	Month	Minimum	Median	Maximum	Interquartile range		Mean	± SD	± SE
Mature hedge	16	April	1.38	2.18	4.01	1.80	2.63	2.40	0.82	0.20
	16	July	2.26	3.76	5.39	3.26	4.44	3.82	0.90	0.23
	16	September	2.25	3.77	4.79	3.45	4.16	3.76	0.66	0.17
New hedge	16	April	1.18	1.76	4.76	1.51	2.11	1.92	0.92	0.23
	16	July	1.08	2.93	3.62	2.61	3.43	2.86	0.70	0.17
	15	September	1.61	3.83	4.94	3.00	4.08	3.59	0.85	0.22
Hedgeless	4	April	2.21	3.06	3.46	2.68	3.32	2.95	0.56	0.28
	4	July	2.82	3.05	3.26	2.88	3.22	3.05	0.22	0.11
	4	September	2.96	3.92	4.34	3.66	4.04	3.78	0.59	0.29

Table B21. Shannon five number summary and mean numbers (± SD & ± SE) of invertebrate groups collected from all boundary types (Mature hedges, New hedges and Hedgeless boundaries) during April, July and September 2011

Boundary type	n	Month	Minimum	Median	Maximum	Interquartile range		Mean	± SD	± SE
Mature hedge	16	April	1.08	1.60	2.02	1.40	1.75	1.58	0.28	0.07
	16	July	1.69	2.08	2.21	1.97	2.14	2.03	0.15	0.04
	16	September	1.76	2.07	2.19	1.90	2.15	2.01	0.14	0.04
New hedge	16	April	0.67	1.28	2.07	1.03	1.42	1.30	0.41	0.10
	16	July	0.40	1.85	2.05	1.77	1.94	1.76	0.39	0.10
	15	September	1.35	1.98	2.09	1.89	2.04	1.94	0.18	0.05
Hedgeless	4	April	1.70	1.74	1.92	1.72	1.79	1.77	0.10	0.05
	4	July	1.82	1.87	1.93	1.84	1.91	1.87	0.05	0.03
	4	September	1.81	1.95	2.03	1.89	2.00	1.94	0.10	0.05

Table B22. Heip five number summary and mean numbers (± SD & ± SE) of invertebrate groups collected from all boundary types (Mature hedges, New hedges and Hedgeless boundaries) during April, July and September 2011

Boundary type	n	Month	Minimum	Median	Maximum	Interquartile range		Mean	± SD	± SE
Mature hedge	16	April	0.20	0.33	0.63	0.29	0.45	0.38	0.13	0.03
	16	July	0.38	0.56	0.70	0.49	0.61	0.55	0.10	0.02
	16	September	0.39	0.56	0.66	0.48	0.61	0.54	0.09	0.02
New hedge	16	April	0.08	0.26	0.85	0.19	0.30	0.31	0.21	0.05
	16	July	0.04	0.43	0.63	0.40	0.46	0.42	0.12	0.03
	15	September	0.24	0.55	0.71	0.50	0.63	0.55	0.12	0.03
Hedgeless	4	April	0.42	0.54	0.59	0.48	0.58	0.52	0.08	0.04
	4	July	0.46	0.53	0.59	0.48	0.58	0.53	0.07	0.03
	4	September	0.43	0.56	0.63	0.50	0.60	0.54	0.09	0.04

Table B23. Simpson (diversity) five number summary and mean numbers (± SD & ± SE) of invertebrate groups collected from all boundary types (Mature hedges, New hedges and Hedgeless boundaries) during April, July and September 2011

Boundary type	n	Month	Minimum	Median	Maximum	Interquartile range		Mean	± SD	± SE
Mature hedge	16	April	1.85	3.17	6.42	2.67	4.15	3.67	1.44	0.36
	16	July	4.09	6.49	7.78	5.34	6.99	6.20	1.17	0.29
	16	September	4.04	6.45	7.76	5.52	7.10	6.21	1.12	0.28
New hedge	16	April	1.38	2.42	7.49	1.71	2.95	2.96	1.84	0.46
	16	July	1.16	4.84	6.38	4.27	5.30	4.61	1.28	0.32
	15	September	2.41	6.20	7.00	5.53	6.46	5.80	1.14	0.29
Hedgeless	4	April	3.87	4.73	5.77	4.30	5.20	4.77	0.81	0.41
	4	July	4.80	5.08	5.53	4.93	5.27	5.12	0.32	0.16
	4	September	4.87	6.12	6.53	5.59	6.44	5.91	0.76	0.38

Table B24. Simpson (evenness) five number summary and mean numbers (± SD & ± SE) of invertebrate groups collected from all boundary types (Mature hedges, New hedges and Hedgeless boundaries) during April, July and September 2011

Boundary type	n	Month	Minimum	Median	Maximum	Interquartile range		Mean	± SD	± SE
Mature hedge	16	April	0.19	0.28	0.56	0.22	0.38	0.31	0.12	0.03
	16	July	0.27	0.49	0.62	0.41	0.54	0.47	0.10	0.03
	16	September	0.29	0.47	0.60	0.42	0.54	0.47	0.09	0.02
New hedge	16	April	0.11	0.21	0.83	0.18	0.25	0.28	0.20	0.05
	16	July	0.10	0.36	0.53	0.32	0.40	0.35	0.10	0.02
	15	September	0.19	0.48	0.63	0.41	0.58	0.48	0.12	0.03
Hedgeless	4	April	0.37	0.46	0.56	0.38	0.53	0.46	0.09	0.05
	4	July	0.37	0.44	0.55	0.42	0.48	0.45	0.08	0.04
	4	September	0.44	0.52	0.53	0.49	0.53	0.50	0.04	0.02

Table B25. Results of Spearman's rho correlations between hedgerow age (years) and invertebrate diversity at ground level for all months combined and individually (April, July, September) for all hedges (n = 32). Values are r_s plus significance values. Significant values are highlighted in bold. An FDR (Benjamini and Yekultieli) corrected significance level of 0.020 applies

Diversity measure	All months (n = 95)		April (n = 32)		July (n = 32)		September (n = 31)	
	r_s	p	r_s	p	r_s	p	r_s	p
Taxon Richness	0.135	0.192	0.187	0.307	-0.009	0.961	0.253	0.170
Berger-Parker	0.121	0.241	0.205	0.260	**0.433**	**0.013**	-0.054	0.774
Shannon	0.193	0.061	0.213	0.242	**0.478**	**0.006**	0.163	0.382
Heip (evenness)	0.100	0.333	0.216	0.236	**0.419**	**0.017**	-0.081	0.666
Simpson (diversity)	0.152	0.140	0.162	0.375	**0.487**	**0.005**	0.080	0.669
Simpson (evenness)	0.090	0.384	0.132	0.472	**0.448**	**0.010**	-0.126	0.498

Table B26. Results of Spearman's rho correlations between hedgerow age (years) and invertebrate diversity at ground level for all months combined and individually (April, July, September) for New hedges only (n = 16). Values are r_s plus significance values. Significant values are highlighted in bold. An FDR (Benjamini and Yekultieli) corrected significance level of 0.020 applies

Diversity measure	All months (n = 47)		April (n = 16)		July (n = 16)		September (n = 15)	
	r_s	p	r_s	p	r_s	p	r_s	p
Taxon Richness	-0.091	0.544	-0.105	0.700	0.203	0.450	-0.443	0.098
Berger-Parker	-0.280	0.057	-0.276	0.300	-0.313	0.238	-0.307	0.266
Shannon (diversity)	-0.212	0.153	-0.346	0.189	-0.194	0.471	-0.179	0.522
Heip (evenness)	-0.168	0.258	-0.244	0.363	-0.296	0.266	0.221	0.429
Simpson (diversity)	-0.239	0.106	-0.335	0.205	-0.265	0.322	-0.331	0.228
Simpson (evenness)	-0.198	0.182	-0.235	0.381	-0.368	0.160	0.022	0.938

Table B27. Spearman's rank correlations between taxonomic abundance and diversity measures for invertebrates collected at ground level. All boundaries (Mature hedges, New hedges and Hedgeless), all months combined (n = 107). B-Y FDR Corrected significance level of 0.010 applies

		Taxon Richness	Berger-Parker	Shannon	Simpson	Simpson Evenness	Heip Evenness
Acari	r_s	0.218	-0.097	-0.100	-0.143	-0.210	-0.214
	p	0.024	0.320	0.307	0.143	0.030	0.027
Araneae	r_s	0.042	0.008	0.055	0.021	0.038	0.002
	p	0.664	0.931	0.576	0.831	0.697	0.987
Coleoptera	r_s	0.116	0.057	0.117	0.102	0.072	0.075
	p	0.234	0.563	0.229	0.294	0.459	0.445
Collembola	r_s	**-0.248**	**-0.575**	**-0.574**	**-0.597**	**-0.572**	**-0.567**
	p	**0.010**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Dermaptera	r_s	0.447	0.111	**0.304**	0.225	0.085	0.108
	p	**<0.001**	0.255	**0.001**	0.020	0.385	0.266
Diptera	r_s	0.196	**0.248**	0.242	0.235	0.187	0.200
	p	0.043	**0.010**	0.012	0.015	0.054	0.039
Hemiptera	r_s	**0.305**	**0.283**	0.353	**0.313**	0.238	**0.253**
	p	**0.001**	**0.003**	**<0.001**	**0.001**	0.014	**0.009**
Hymenoptera (all)	r_s	**0.407**	0.175	0.189	0.148	0.037	0.066
	p	**<0.001**	0.071	0.051	0.127	0.703	0.501
Hymenoptera (Parasitica)	r_s	**0.461**	**0.374**	**0.391**	**0.348**	0.234	0.230
	p	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.015	0.017
Isopoda	r_s	**0.399**	0.145	.220*	0.148	0.028	0.117
	p	**0.001**	0.137	0.023	0.129	0.777	0.229
Julida	r_s	0.417	0.052	0.113	0.059	-0.076	-0.074
	p	**<0.001**	0.597	0.248	0.545	0.439	0.451
Lepidoptera	r_s	**0.309**	-0.146	-0.133	-0.193	**-0.271**	**-0.251**
	p	**0.001**	0.133	0.172	0.046	**0.005**	**0.009**
Opiliones	r_s	**0.406**	**0.433**	**0.459**	**0.431**	**0.298**	**0.341**
	p	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.002**	**<0.001**
Psocoptera	r_s	**0.339**	**0.274**	**0.375**	**0.344**	0.208	0.230
	p	**<0.001**	**0.004**	**<0.001**	**<0.001**	0.032	0.017
Pulmonata	r_s	0.393	-0.026	0.013	-0.013	-0.144	-0.163
	p	**<0.001**	0.790	0.892	0.891	0.140	0.093
Thysanoptera	r_s	0.149	-0.070	0.052	-0.005	-0.078	-0.072
	p	0.127	0.474	0.593	0.956	0.426	0.463

Table B28. Spearman's rank correlations between individual taxa collected at ground level and diversity measures. Hedges only, all months combined (n = 95). B-Y FDR Corrected significance level of 0.010 applies

		Taxon Richness	Berger-Parker	Shannon	Simpson	Heip Evenness	Simpson Evenness
Acari	r_s	0.248	-0.080	-0.091	-0.132	-0.231	-0.194
	p	0.016	0.443	0.381	0.204	0.024	0.059
Araneae	r_s	0.159	0.011	0.087	0.033	-0.045	-0.005
	p	0.125	0.915	0.400	0.748	0.662	0.961
Coleoptera	r_s	0.126	0.058	0.121	0.104	0.063	0.081
	p	0.224	0.575	0.241	0.318	0.543	0.436
Collembola	r_s	**-0.262**	**-0.580**	**-0.577**	**-0.599**	**-0.614**	**-0.588**
	p	**0.010**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Dermaptera	r_s	**0.426**	0.133	**0.309**	0.241	0.171	0.141
	p	**<0.001**	0.200	**0.002**	0.019	0.098	0.174
Diptera	r_s	0.234	0.245	0.253	0.242	0.198	0.202
	p	0.022	0.017	0.014	0.018	0.054	0.050
Hemiptera	r_s	**0.366**	**0.326**	**0.406**	**0.365**	**0.284**	**0.292**
	p	**<0.001**	**0.001**	**<0.001**	**<0.001**	**0.005**	**0.004**
Hymenoptera (all)	r_s	**0.428**	0.177	0.179	0.141	0.084	0.056
	p	**<0.001**	0.087	0.083	0.171	0.417	0.588
Hymenoptera (Parasitica)	r_s	**0.505**	**0.402**	**0.402**	**0.367**	0.260	**0.279**
	p	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.011	**0.006**
Isopoda	r_s	**0.396**	0.182	0.257	0.184	0.141	0.075
	p	**<0.001**	0.078	0.012	0.074	0.174	0.471
Julida	r_s	**0.416**	0.059	0.117	0.062	-0.023	-0.048
	p	**<0.001**	0.570	0.259	0.552	0.824	0.643
Lepidoptera	r_s	**0.308**	-0.165	-0.171	-0.221	-0.236	-0.270
	p	**0.002**	0.109	0.097	0.032	0.021	0.008
Opiliones	r_s	**0.458**	**0.442**	**0.471**	**0.441**	**0.362**	**0.319**
	p	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.002**
Psocoptera	r_s	**0.305**	**0.303**	**0.394**	**0.368**	**0.276**	**0.265**
	p	**0.003**	**0.003**	**<0.001**	**<0.001**	**0.007**	**0.009**
Pulmonata	r_s	**0.382**	-0.048	-0.013	-0.034	-0.144	-0.133
	p	**<0.001**	0.642	0.899	0.742	0.163	0.198
Thysanoptera	r_s	0.112	-0.028	0.074	0.029	-0.034	-0.016
	p	0.282	0.790	0.477	0.777	0.747	0.875

Table B29. Diversity values for superfamilies/families of Coleoptera and Diptera for Mature Hedges (n = 16), New Hedges (n = 16) and Hedgeless boundaries (n = 4), based on combined totals for: April; July; September. Based on the number of taxa found in all hedges/boundaries totalled by hedge/boundary type and month

	Mature Hedges	New Hedges	Hedgeless boundaries	Mature Hedges	New Hedges	Hedgeless boundaries	Mature Hedges	New Hedges	Hedgeless boundaries
	APRIL			JULY			SEPTEMBER		
Coleoptera									
No. of taxa	20	15	9	19	18	11	12	11	8
Berger-Parker	5.52	3.22	2.26	2.93	3.05	2.89	3.50	2.93	2.17
Shannon	2.19	1.97	1.50	1.81	1.85	1.90	1.84	1.69	1.43
Simpson (Diversity)	7.37	5.47	3.33	4.44	4.80	5.29	5.02	3.92	3.10
Heip (Evenness)	0.42	0.44	0.43	0.28	0.31	0.57	0.48	0.44	0.45
Simpson (Evenness)	0.37	0.36	0.37	0.23	0.27	0.48	0.42	0.36	0.39
Diptera									
No. of taxa	18	16	10	28	26	23	24	19	15
Berger-Parker	1.84	2.11	2.50	2.66	3.50	2.74	3.13	3.96	2.95
Shannon	1.56	1.74	1.62	2.12	2.26	2.16	1.03	0.99	1.11
Simpson (Diversity)	2.91	3.58	3.83	4.87	6.25	4.80	5.13	5.67	4.81
Heip (Evenness)	0.22	0.31	0.45	0.27	0.34	0.35	0.08	0.09	0.14
Simpson (Evenness)	0.16	0.22	0.38	0.17	0.24	0.21	0.21	0.30	0.32

Appendix C. Supplementary information relating to Chapter 5

Table C1. Total abundances of canopy-active invertebrates per hedge type (Mature and New) and month (April, July, September): all taxa – 2011

Hedge type	Month	Total Abundance
Mature (n=13)	April	1,106
New (n=13)	April	1,362
Mature (n=15)	July	3,720
New (n=16)	July	3,004
Mature (n=13)	Sept	1,368
New (n=13)	Sept	1,105
Mature (all months)		**6,194**
New Total (all months)		**5,471**
Grand Total		**11,665**

Table C2. Overview of the frequency/abundance (mean per hedge) of individual taxa for both hedge types (Mature and New) over time (Month: April, July, September)

Taxon	Mature hedges			New hedges		
	April n = 13	July n = 15	Sept. n = 13	April n = 13	July n = 16	Sept. n = 13
Acari	14.00	23.53	5.85	3.08	15.69	1.08
Araneae	5.92	17.4	13.15	13.31	13.31	16.46
Coleoptera	30.85	17.4	17.15	25.23	30.69	8
Collembola	16.77	79.87	33.85	43.38	78.56	30.62
Dermaptera	0.15	0.93	1.69	0.31	0.69	0.62
Diptera	4.08	3.33	2.31	5.69	1.75	1.77
Hemiptera	7.15	63.47	9.92	6	18.06	8.08
Hymenoptera	2.31	15.8	8.23	5.31	9	9.15
Isopoda	0	0.13	0.15	0	0.06	0
Julida	0	0.07	0.54	0	0	0
Lepidoptera	1.85	1.8	0.54	0.69	0.88	0.31
Neuroptera	0.08	0.47	0.08	0.08	0	0.15
Opiliones	0	0.87	1.77	0.08	0.38	0.92
Polyxenida	0	0.13	0	0	0	0
Psocoptera	0.08	8.2	9.08	0.15	4.81	6.46
Pulmonata	0	1.07	0.38	0.15	2.19	0.85
Thysanoptera	1.85	13.53	0.54	1.31	11.69	0.54
No. of taxa	12	17	16	14	14	14

Table C3. Beatings – canopy-active invertebrate abundances by taxon showing total and mean values per hedge (± SD, ± SE) for Mature and New hedges – April 2011

	Mature hedges (n = 13)				New hedges (n = 13)			
Taxon	**Total**	**Mean**	**+/- SD**	**+/- SE**	**Total**	**Mean**	**+/- SD**	**+/- SE**
Coleoptera	401	30.85	24.50	6.80	328	25.23	19.72	5.47
Collembola	218	16.77	21.66	6.01	564	43.38	96.99	26.90
Acari	182	14.00	11.93	3.31	40	3.08	3.86	1.07
Hemiptera	93	7.15	4.72	1.31	78	6.00	6.10	1.69
Araneae	77	5.92	3.43	0.95	173	13.31	7.63	2.12
Diptera	53	4.08	4.41	1.22	74	5.69	9.65	2.68
Hymenoptera	30	2.31	2.56	0.71	69	5.31	4.15	1.15
Thysanoptera	24	1.85	2.15	0.60	17	1.31	1.93	0.54
Lepidoptera	24	1.85	2.82	0.78	9	0.69	1.03	0.29
Dermaptera	2	0.15	0.55	0.15	4	0.31	0.85	0.24
Psocoptera	1	0.08	0.28	0.08	2	0.17	0.39	0.11
Neuroptera	1	0.08	0.28	0.08	1	0.08	0.28	0.08
Pulmonata	0	0	0	0	2	0.15	0.38	0.10
Opiliones	0	0	0	0	1	0.08	0.28	0.08
Polyxenida	0	0	0	0	0	0	0	0
Isopoda	0	0	0	0	0	0	0	0
Julida	0	0	0	0	0	0	0	0

Table C4. Beatings – canopy-active invertebrate abundances by taxon showing total and mean values per hedge (± SD, ± SE) for Mature and New hedges – July 2011

	Mature hedges (n = 15)				New hedges (n = 16)			
Taxon	**Total**	**Mean**	**+/- SD**	**+/- SE**	**Total**	**Mean**	**+/- SD**	**+/- SE**
Collembola	1198	79.87	119.86	30.95	1257	78.56	114.80	28.70
Hemiptera	952	63.47	120.50	31.11	289	18.06	18.08	4.52
Acari	353	23.53	28.17	7.27	251	15.69	20.30	5.07
Coleoptera	261	17.40	9.42	2.43	491	30.69	29.47	7.37
Araneae	261	17.40	18.13	4.68	213	13.31	7.32	1.83
Hymenoptera	237	15.80	18.39	4.75	144	9.00	7.03	1.76
Thysanoptera	203	13.53	10.04	2.59	187	11.69	7.68	1.92
Psocoptera	123	8.20	12.81	3.31	77	4.81	5.41	1.35
Diptera	50	3.33	4.56	1.18	28	1.75	2.08	0.52
Lepidoptera	27	1.80	1.57	0.40	14	0.88	1.26	0.31
Pulmonata	16	1.07	1.98	0.51	35	2.19	2.26	0.56
Dermaptera	14	0.93	1.39	0.36	11	0.69	1.14	0.28
Opiliones	13	0.87	1.19	0.31	6	0.38	0.72	0.18
Neuroptera	7	0.47	0.92	0.24	0	0	0	0
Polyxenida	2	0.13	0.52	0.13	0	0	0	0
Isopoda	2	0.13	0.35	0.09	1	0.06	0.25	0.06
Julida	1	0.07	0.26	0.07	0	0	0	0

Table C5. Beatings – canopy-active invertebrate abundances by taxon showing total and mean values per hedge (± SD, ± SE) for Mature and New hedges – September 2011

	Mature hedges (n = 13)				New hedges (n = 13)			
Taxon	**Total**	**Mean**	**+/- SD**	**+/- SE**	**Total**	**Mean**	**+/- SD**	**+/- SE**
Collembola	440	33.85	57.61	15.98	398	30.62	46.88	13.00
Coleoptera	223	17.15	17.22	4.78	104	8.00	8.26	2.29
Araneae	171	14.25	18.47	5.12	214	16.46	13.04	3.62
Hemiptera	129	9.92	10.28	2.85	105	8.08	15.05	4.17
Psocoptera	118	9.08	12.34	3.42	84	6.46	8.20	2.27
Hymenoptera	107	8.23	15.02	4.17	119	9.15	15.21	4.22
Acari	76	6.33	12.05	3.34	14	1.08	1.75	0.49
Diptera	30	2.31	5.15	1.43	23	1.77	2.74	0.76
Opiliones	23	1.77	1.79	0.50	12	0.92	1.04	0.29
Dermaptera	22	1.69	2.63	0.73	8	0.62	0.65	0.18
Thysanoptera	7	0.58	0.90	0.25	7	0.54	0.66	0.18
Lepidoptera	7	0.54	1.39	0.39	4	0.31	0.48	0.13
Julida	7	0.54	1.45	0.40	0	0	0	0
Pulmonata	5	0.38	0.77	0.21	11	0.85	1.21	0.34
Isopoda	2	0.15	0.55	0.15	0	0	0	0
Neuroptera	1	0.08	0.28	0.08	2	0.15	0.38	0.10
Polyxenida	0	0	0	0	0	0	0	0

Table C6. Families/superfamilies of Coleoptera found by beating in Mature hedges and New hedges, April 2011. Abundance and relative % of Coleopteran assemblage shown

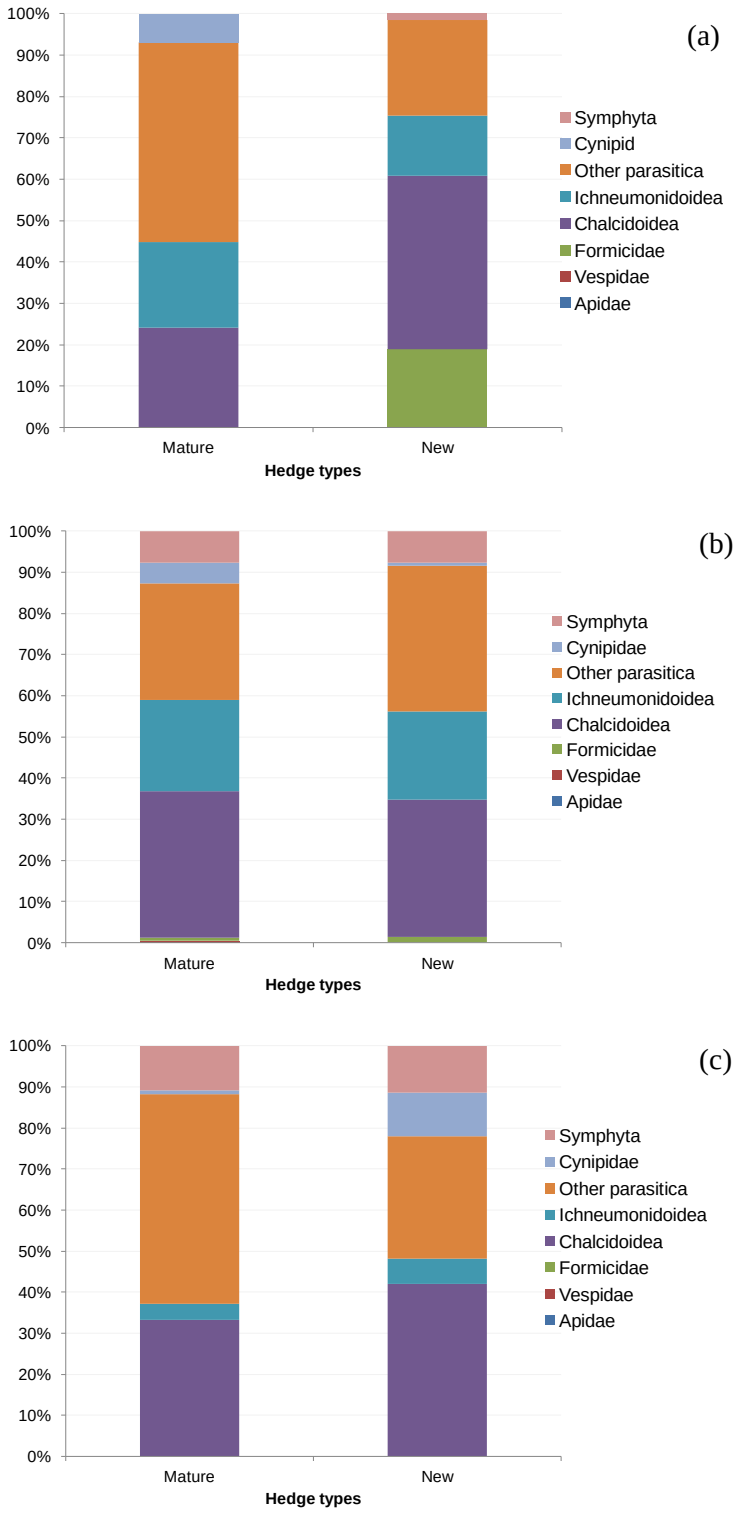
	Mature hedges		New hedges	
Family/superfamily	**Abundance**	**% of order**	**Abundance**	**% of order**
Cantharidae	1	0.2	5	2
Carabidae	4	1	7	2
Cerambycidae	0	0	1	0.3
Chrysomelidae	125	31	43	13
Coccinelidae	11	3	31	9
Corylophidae	2	0.5	0	0
Cryptophagidae	1	0.2	3	1
Curculionoidea	37	9	31	9
Elateridae	1	0.2	1	0.3
Latridiidae	200	50	188	57
Melandryidae	0	0	1	0.3
Nitidulidae	10	2	11	3
Phalacridae	1	0.2	1	0.3
Staphylinidae	6	1	4	1
Adult (unidentified)	0	0	0	0
Larval (unidentified)	2	0.5	1	0.3
Total Coleoptera	**401**	**100%**	**328**	**100%**

Table C7. Families/superfamilies of Coleoptera found by beating in Mature hedges and New hedges, July 2011. Abundance and relative % of Coleopteran assemblage shown

	Mature hedges		New hedges	
Family/superfamily	Abundance	% of order	Abundance	% of order
Cantharidae	0	0	1	0.2
Carabidae	2	1	2	0.4
Chrysomelidae	14	5	14	3
Coccinelidae	2	1	8	2
Cryptophagidae	8	3	12	2
Curculionoidea	83	32	282	57
Elateridae	0	0	1	0.2
Latridiidae	97	37	145	30
Nitidulidae	25	10	5	1
Phalacridae	1	0.4	2	0.4
Ptilidae	0	0	1	0.2
Staphylinidae	1	0.4	6	1
Tenebrionidae	24	9	6	1
Adult (unidentified)	2	1	0	0
Larval (unidentified)	2	1	6	1
Total Coleoptera	**261**	**100%**	**491**	**100%**

Table C8. Families/superfamilies of Coleoptera found by beating in Mature hedges and New hedges, September 2011. Abundance and relative % of Coleopteran assemblage shown

	Mature hedges		New hedges	
Family/superfamily	Abundance	% of order	Abundance	% of order
Aderidae	0	0	1	1
Carabidae	24	11	4	4
Chrysomelidae	33	15	19	18
Coccinellidae	15	7	33	32
Cryptophagidae	0	0	2	2
Curculionoidea	38	17	22	21
Latridiidae	103	46	23	22
Phalacridae	3	1	0	0
Staphylinidae	7	3	0	0
Adult (unidentified)	0	0	0	0
Larval (unidentified)	0	0	0	0
Total Coleoptera	**223**	**100%**	**104**	**100%**



Figures C1 (a)–(c). Stacked column charts showing the proportional abundance of sub-classifications of Hymenoptera in Mature hedges and New hedges for: (a) April, (b) July and (c) September. Categories shown highlight differences in splits between Formicidae and Parasitica (Ichneumonidoidea, Chalcidoidea, Cynipidae and Other Parasitica) and other groups

Table C9. Families/superfamilies of Diptera found by beating in Mature hedges and New hedges, April 2011. Abundance and relative % of Dipteran assemblage shown

		Mature hedges		New hedges	
Suborder	Family/superfamily	Abundance	% of order	Abundance	% of order
Brachycera	Empididae	4	8	6	8
Brachycera	Ephydridae	0	0	1	1
Brachycera	Other Brachycera	0	0	2	3
Brachycera	Platystomatidae	0	0	1	1
Nematocera	Bibionidae	0	0	19	26
Nematocera	Cecidomyiidae	2	4	20	27
Nematocera	Ceratopogonidae	0	0	2	3
Nematocera	Other Nematocera	7	13	3	4
Nematocera	Psychodidae	0	0	1	1
Nematocera	Scatopsidae	1	2	3	4
Nematocera	Sciaridae	39	74	16	22
Unidentified	Adult (unidentified)	0	0	0	0
Unidentified	Larval (unidentified)	0	0	0	0
	Total Diptera	**53**	**100%**	**74**	**100%**

Table C10. Families/superfamilies of Diptera found by beating in Mature hedges and New hedges, July 2011. Abundance and relative % of Dipteran assemblage shown

		Mature hedges		New hedges	
Suborder	Family/superfamily	Abundance	% of order	Abundance	% of order
Brachycera	Chloropidae	1	2	0	0
Brachycera	Dolichopopidae	5	10	1	4
Brachycera	Empididae	1	2	1	4
Brachycera	Muscidae	0	0	1	4
Brachycera	Opomyzidae	2	4	0	0
Brachycera	Phoridae	1	2	2	7
Brachycera	Sciomyzidae	1	2	0	0
Brachycera	Syrphidae	2	4	0	0
Brachycera	Other Brachycera	21	42	5	18
Nematocera	Other Nematocera	7	14	4	14
Nematocera	Psychodidae	2	4	0	0
Nematocera	Scatopsidae	0	0	1	4
Nematocera	Sciaridae	3	6	9	32
Nematocera	Tipulidae	1	2	0	0
Unidentified	Adult	1	2	0	0
Unidentified	Larval	2	4	4	14
	Total Diptera	**50**	**100%**	**28**	**100%**

Table C11. Families/superfamilies of Diptera found by beating in Mature hedges and New hedges, September 2011. Abundance and relative % of Dipteran assemblage shown

September		Mature hedges		New hedges	
Suborder	Family/superfamily	Abundance	% of order	Abundance	% of order
Brachycera	**Other Brachycera**	0	0	3	13
Brachycera	**Phoridae**	1	3	0	0
Brachycera	**Sphaeroceridae**	1	3	0	0
Brachycera	**Syrphidae**	0	0	3	13
Nematocera	**Ceratopogonidae**	0	0	2	9
Nematocera	**Culicidae**	1	3	1	4
Nematocera	**Mycetophilidae**	1	3	0	0
Nematocera	**Other Nematocera**	5	17	3	13
Nematocera	**Psychodidae**	0	0	4	17
Nematocera	**Scatopsidae**	12	40	0	0
Nematocera	**Sciaridae**	8	27	6	26
Unidentified	**Adult**	0	0	0	0
Unidentified	**Larval**	1	3	1	4
	Total Diptera	**30**	**100%**	**23**	**100%**

Table C12. Results of Spearman's rho correlations between hedgerow age (years) and abundance of canopy-active taxa (both in total and for each individual taxon) for all months combined and individually (April, July, September). Values are r_s plus significance values. Significant values are in bold. A Benjamini –Yekultieli method FDR corrected significance level of 0.015 applies

Taxon	All months (n = 83)		April (n = 26)		July (n = 31)		Sept (n = 26)	
	r_s	p	r_s	p	r_s	p	r_s	p
All taxa – total	0.062	0.580	0.073	0.722	0.330	0.069	-0.144	0.482
Acari	0.266	0.016	0.459	0.018	0.367	0.042	0.177	0.386
Araneae	-0.192	0.082	**-0.474**	**0.015**	0.055	0.768	-0.227	0.264
Coleoptera	0.155	0.161	0.122	0.554	0.178	0.338	0.172	0.400
Collembola	-0.045	0.686	0.112	0.584	0.092	0.621	0.036	0.860
Dermaptera	0.012	0.918	*		0.024	0.898	0.062	0.763
Diptera	0.085	0.442	0.129	0.531	0.278	0.130	-0.185	0.367
Hemiptera	0.113	0.308	0.083	0.688	0.351	0.053	0.005	0.979
Hymenoptera	-0.102	0.358	-0.429	0.029	0.324	0.075	-0.231	0.256
Isopoda	Too few specimens distributed in too few hedges for meaningful analysis**							
Julida	Too few specimens distributed in too few hedges for meaningful analysis**							
Lepidoptera	0.212	0.055	0.268	0.186	0.379	0.035	-0.066	0.750
Neuroptera	Too few specimens distributed in too few hedges for meaningful analysis*							
Opiliones	0.022	0.840	*		0.100	0.593	-0.001	0.997
Polyxenida	Too few specimens distributed in too few hedges for meaningful analysis**							
Psocoptera	0.038	0.735	*		0.232	0.208	0.174	0.394
Pulmonata	-0.187	0.091	*		-0.209	0.259	0.100	0.628
Thysanoptera	-0.005	0.964	0.026	0.900	0.073	0.698	-0.072	0.726

* Asterisks indicate taxa represented by fewer than 10 individuals and collected from ≤ 3 hedges respectively in April. Abundance data carried many zero values. Correlations were not conducted

** These taxa never exceeded 10 individuals for any month and were never collected from more than 4 hedges respectively. Their abundance data contained many zero values

Table C13. Results of Spearman's rho correlations between hedgerow age (years) and abundance of canopy-active taxa (both in total and for each individual taxon) for all months combined and individually (April, July, September) for New hedges only. Values are r_s plus significance values. Significant values are highlighted in bold. A Benjamini –Yekultieli method FDR corrected significance level of 0.015 applies

Taxon	All months (n = 42)		April (n = 13)		July (n = 16)		Sept (n = 13)	
	r_s	p	r_s	p	r_s	p	r_s	p
All taxa – total	-0.025	0.877	-0.168	0.582	0.437	0.090	-0.258	0.395
Acari	-0.051	0.749	-0.149	0.626	0.343	0.193	-0.395	0.181
Araneae	0.077	0.630	0.145	0.637	-0.034	0.900	0.223	0.464
Coleoptera	0.210	0.181	0.115	0.709	0.445	0.084	-0.147	0.632
Collembola	0.064	0.686	0.090	0.769	0.403	0.122	-0.081	0.790
Dermaptera	-0.113	0.476	*		-0.248	0.354	-0.151	0.622
Diptera	-0.132	0.406	-0.029	0.924	0.232	0.386	0.660	0.014
Hemiptera	-0.272	0.081	-0.396	0.181	-0.027	0.922	-0.483	0.094
Hymenoptera	-0.246	0.116	-0.303	0.315	0.069	0.799	-0.428	0.145
Isopoda	Too few specimens distributed in too few hedges for meaningful analysis**							
Julida	Too few specimens distributed in too few hedges for meaningful analysis**							
Lepidoptera	-0.080	0.616	-0.005	0.987	0.078	0.774	****	
Neuroptera	Too few specimens distributed in too few hedges for meaningful analysis**							
Opiliones	**-0.445**	**0.003**	*		***		**-0.703**	**0.007**
Polyxenida	Too few specimens distributed in too few hedges for meaningful analysis**							
Psocoptera	-0.183	0.247	*		0.159	0.557	-0.518	0.070
Pulmonata	0.011	0.944	*		-0.003	0.991	0.482	0.095
Thysanoptera	-0.058	0.716	-0.346	0.247	0.231	0.389	-0.009	0.976

* Fewer than 10 individuals found for each taxon and in ≤ 2 hedges respectively. No correlations

** Collected from ≤ 2 New hedges respectively and present in very low numbers, with many zero values

*** Opiliones found in 4 New hedgerows only in July. No correlations conducted for July

**** Lepidoptera collected in low numbers from 4 hedges only. No correlations conducted for September

Table C14. Correlations between abundances of canopy taxa for all hedgerows (Mature and New) combined (n = 83) and all months combined (April, July, September)

		Acari	Araneae	Coleoptera	Collembola	Dermaptera	Diptera	Hemiptera	Hymenoptera	Lepidoptera	Opiliones	Psocoptera	Pulmonata	Thysanoptera
Acari	r_s		0.266	**0.553**	**0.439**	0.253	**0.391**	**0.482**	**0.316**	**0.297**	0.042	0.223	0.193	**0.417**
	p		0.015	**<0.001**	**<0.001**	0.021	**<0.001**	**<0.001**	**0.004**	**0.006**	0.705	0.042	0.081	**<0.001**
Araneae	r_s	0.266		**0.392**	**0.344**	**0.316**	**0.310**	**0.462**	**0.502**	0.007	0.091	**0.418**	0.224	0.172
	p	0.015		**<0.001**	**0.001**	**0.004**	**0.004**	**<0.001**	**<0.001**	0.951	0.414	**<0.001**	0.042	0.120
Coleoptera	r_s	**0.553**	**0.392**		**0.507**	0.146	**0.486**	**0.402**	**0.457**	0.281	0.085	0.065	-0.133	0.234
	p	**<0.001**	**<0.001**		**<0.001**	0.187	**<0.001**	**<0.001**	**<0.001**	0.010	0.447	0.557	0.229	0.033
Collembola	r_s	**0.439**	**0.344**	**0.507**		0.206	**0.382**	**0.506**	**0.629**	0.130	**0.330**	**0.292**	0.042	**0.343**
	p	**<0.001**	**0.001**	**<0.001**		0.061	**<0.001**	**<0.001**	**<0.001**	0.242	**0.002**	**0.007**	0.709	**0.001**
Dermaptera	r_s	0.253	**0.316**	0.146	0.206		0.180	0.227	0.136	-0.051	**0.333**	**0.369**	0.171	0.033
	p	0.021	**0.004**	0.187	0.061		0.103	0.039	0.221	0.647	**0.002**	**0.001**	0.123	0.765
Diptera	r_s	**0.391**	**0.310**	**0.486**	**0.382**	0.180		**0.354**	**0.401**	0.186	0.098	0.156	-0.077	0.055
	p	**<0.001**	**0.004**	**<0.001**	**<0.001**	0.103		**0.001**	**<0.001**	0.092	0.380	0.158	0.488	0.620
Hemiptera	r_s	**0.482**	**0.462**	**0.402**	**0.506**	0.227	**0.354**		**0.660**	0.243	**0.311**	**0.483**	-0.004	**0.524**
	p	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.039	**0.001**		**<0.001**	0.027	**0.004**	**<0.001**	0.970	**<0.001**
Hymenoptera	r_s	**0.316**	**0.502**	**0.457**	**0.629**	0.136	**0.401**	**0.660**		0.192	**0.347**	**0.358**	-0.035	**0.416**
	p	**0.004**	**<0.001**	**<0.001**	**<0.001**	0.221	**<0.001**	**<0.001**		0.083	**0.001**	**0.001**	0.753	**<0.001**
Lepidoptera	r_s	**0.297**	0.007	0.281	0.130	-0.051	0.186	0.243	0.192		0.103	0.062	0.019	0.134
	p	**0.006**	0.951	0.010	0.242	0.647	0.092	0.027	0.083		0.356	0.579	0.863	0.228
Opiliones	r_s	0.042	0.091	0.085	**0.330**	**0.333**	0.098	**0.311**	**0.347**	0.103		**0.453**	-0.141	-0.015
	p	0.705	0.414	0.447	**0.002**	**0.002**	0.380	**0.004**	**0.001**	0.356		**<0.001**	0.204	0.895
Psocoptera	r_s	0.223	**0.418**	0.065	**0.292**	**0.369**	0.156	**0.483**	**0.358**	0.062	**0.453**		0.207	0.179
	p	0.042	**<0.001**	0.557	**0.007**	**0.001**	0.158	**<0.001**	**0.001**	0.579	**<0.001**		0.060	0.105
Pulmonata	r_s	0.193	0.224	-0.133	0.042	0.171	-0.077	-0.004	-0.035	0.019	-0.141	0.207		0.098
	p	0.081	0.042	0.229	0.709	0.123	0.488	0.970	0.753	0.863	0.204	0.060		0.378
Thysanoptera	r_s	**0.417**	0.172	0.234	**0.343**	0.033	0.055	**0.524**	**0.416**	0.134	-0.015	0.179	0.098	
	p	**<0.001**	0.120	0.033	**0.001**	0.765	0.620	**<0.001**	**<0.001**	0.228	0.895	0.105	0.378	

Table C15. Correlations between abundances of canopy taxa for all hedgerows combined (Mature and New) – April 2011 (n = 26)

APRIL		Acari	Araneae	Coleoptera	Collembola	Diptera	Hemiptera	Hymenoptera	Lepidoptera	Thysanoptera
Acari	r_s		0.012	0.351	0.342	0.075	0.161	-0.083	0.161	-0.010
	p		0.952	0.079	0.087	0.717	0.431	0.688	0.431	0.960
Araneae	r_s	0.012		0.474	0.333	0.194	0.489	**0.696**	0.096	0.143
	p	0.952		0.014	0.097	0.342	0.011	**<0.001**	0.643	0.487
Coleoptera	r_s	0.351	0.474		0.281	0.351	**0.541**	0.373	0.430	0.140
	p	0.079	0.014		0.164	0.079	**0.004**	0.06	0.029	0.495
Collembola	r_s	0.342	0.333	0.281		0.326	0.491	0.425	-0.06	0.254
	p	0.087	0.097	0.164		0.104	0.011	0.031	0.769	0.211
Diptera	r_s	0.075	0.194	0.351	0.326		0.402	0.426	-0.137	0.162
	p	0.717	0.342	0.079	0.104		0.042	0.030	0.504	0.430
Hemiptera	r_s	0.161	0.489	**0.541**	0.491	0.402		0.449	0.270	0.369
	p	0.431	0.011	**0.004**	0.011	0.042		0.022	0.182	0.064
Hymenoptera	r_s	-0.083	**0.696**	0.373	0.425	0.426	0.449		-0.017	0.159
	p	0.688	**<0.001**	0.060	0.031	0.030	0.022		0.934	0.437
Lepidoptera	r_s	0.161	0.096	0.430	-0.060	-0.137	0.270	-0.017		-0.013
	p	0.431	0.643	0.029	0.769	0.504	0.182	0.934		0.951
Thysanoptera	r_s	-0.010	0.143	0.140	0.254	0.162	0.369	0.159	-0.013	
	p	0.960	0.487	0.495	0.211	0.430	0.064	0.437	0.951	

Table C16. Correlations between abundances of canopy taxa for all hedgerows (Mature and New) combined – July 2011 (n = 31)

JULY		Acari	Araneae	Coleoptera	Collembola	Dermaptera	Diptera	Hemiptera	Hymenoptera	Lepidoptera	Opiliones	Psocoptera	Pulmonata	Thysanoptera
Acari	r_s		0.384	**0.612**	0.447	0.267	**0.720**	0.325	0.289	0.402	0.176	**0.530**	0.170	-0.130
	p		0.033	**<0.001**	0.012	0.147	**<0.001**	0.075	0.115	0.025	0.343	**0.002**	0.361	0.486
Aran.	r_s	0.384		0.109	0.056	0.384	0.413	0.047	0.22	-0.045	-0.144	**0.464**	0.279	-0.206
	p	0.033		0.560	0.765	0.033	0.021	0.800	0.235	0.811	0.439	**0.008**	0.128	0.266
Coleo.	r_s	**0.612**	0.109		**0.723**	0.018	0.414	0.019	0.398	0.148	0.214	0.276	-0.112	0.204
	p	**<0.001**	0.560		**<0.001**	0.921	0.021	0.920	0.026	0.426	0.249	0.133	0.547	0.272
Coll.	r_s	0.447	0.056	**0.723**		-0.076	0.413	0.125	**0.565**	0.241	0.323	0.189	-0.101	0.076
	p	0.012	0.765	**<0.001**		0.686	0.021	0.504	**0.001**	0.192	0.076	0.310	0.591	0.684
Derma.	r_s	0.267	0.384	0.018	-0.076		0.213	0.007	-0.118	0.106	0.192	0.239	0.052	-0.214
	p	0.147	0.033	0.921	0.686		0.249	0.97	0.527	0.570	0.301	0.196	0.781	0.247
Dip.	r_s	**0.720**	0.413	0.414	0.413	0.213		0.106	0.264	0.428	0.064	**0.461**	0.191	-0.399
	p	**<0.001**	0.021	0.021	0.021	0.249		0.57	0.152	0.016	0.731	**0.009**	0.303	0.026
Hemi.	r_s	0.325	0.047	0.019	0.125	0.007	0.106		0.43	0.238	0.284	0.300	-0.247	0.204
	p	0.075	0.800	0.92	0.504	0.970	0.570		0.016	0.197	0.121	0.100	0.181	0.271
Hymeno.	r_s	0.289	0.22	0.398	**0.565**	-0.118	0.264	0.430		0.154	0.492	0.115	-0.403	0.411
	p	0.115	0.235	0.026	**0.001**	0.527	0.152	0.016		0.409	0.005	0.537	0.025	0.022
Lepido.	r_s	0.402	-0.045	0.148	0.241	0.106	0.428	0.238	0.154		0.364	0.206	0.085	-0.049
	p	0.025	0.811	0.426	0.192	0.570	0.016	0.197	0.409		0.044	0.267	0.651	0.794
Opilio.	r_s	0.176	-0.144	0.214	0.323	0.192	0.064	0.284	0.492	0.364		-0.085	-0.338	0.183
	p	0.343	0.439	0.249	0.076	0.301	0.731	0.121	0.005	0.044		0.651	0.063	0.323
Psoco.	r_s	**0.530**	**0.464**	0.276	0.189	0.239	**0.461**	0.300	0.115	0.206	-0.085		0.183	-0.072
	p	**0.002**	**0.008**	0.133	0.310	0.196	**0.009**	0.100	0.537	0.267	0.651		0.323	0.702
Pulm.	r_s	0.170	0.279	-0.112	-0.101	0.052	0.191	-0.247	-0.403	0.085	-0.338	0.183		-0.466
	p	0.361	0.128	0.547	0.591	0.781	0.303	0.181	0.025	0.651	0.063	0.323		0.008
Thysano.	r_s	-0.130	-0.206	0.204	0.076	-0.214	-0.399	0.204	0.411	-0.049	0.183	-0.072	-0.466	
	p	0.486	0.266	0.272	0.684	0.247	0.026	0.271	0.022	0.794	0.323	0.702	0.008	

Table C17. Correlations between abundances of canopy taxa for all hedgerows combined (Mature and New) – September 2011 (n = 26)

SEPTEMBER		Acari	Araneae	Coleoptera	Collembola	Dermaptera	Diptera	Hemiptera	Hymenoptera	Lepidoptera	Opiliones	Psocoptera	Pulmonata	Thysanoptera
Acari	r_s		0.237	**0.534**	0.341	0.435	0.519	0.395	0.312	-0.096	0.326	0.481	0.09	0.424
	p		0.245	**0.005**	0.088	0.026	0.007	0.046	0.121	0.640	0.105	0.013	0.662	0.031
Aran.	r_s	0.237		**0.666**	0.48	0.291	0.429	**0.662**	**0.608**	-0.042	0.185	**0.639**	0.077	0.382
	p	0.245		**<0.001**	0.013	0.149	0.029	**<0.001**	**0.001**	0.838	0.365	**<0.001**	0.707	0.054
Coleo.	r_s	**0.534**	**0.666**		**0.617**	**0.500**	**0.557**	**0.722**	**0.631**	0.163	0.443	**0.661**	-0.229	0.233
	p	**0.005**	**<0.001**		**0.001**	**0.009**	**0.003**	**<0.001**	**0.001**	0.427	0.023	**<0.001**	0.261	0.253
Coll.	r_s	0.341	0.480	0.617		0.354	0.521	0.545	0.663	0.179	0.427	0.578	-0.17	0.307
	p	0.088	0.013	0.001		0.076	0.006	0.004	<0.001	0.382	0.030	0.002	0.406	0.127
Derma.	r_s	0.435	0.291	0.5	0.354		0.362	0.208	0.203	0.062	0.224	0.338	0.192	0.235
	p	0.026	0.149	0.009	0.076		0.069	0.307	0.32	0.763	0.271	0.091	0.347	0.249
Dip.	r_s	**0.519**	0.429	**0.557**	**0.521**	0.362		**0.720**	**0.640**	0.236	0.434	**0.727**	-0.314	**0.525**
	p	**0.007**	0.029	**0.003**	**0.006**	0.069		**<0.001**	**<0.001**	0.246	0.027	**<0.001**	0.119	**0.006**
Hemi.	r_s	0.395	**0.662**	**0.722**	**0.545**	0.208	**0.720**		**0.743**	0.151	**0.506**	**0.774**	-0.388	0.286
	p	0.046	**<0.001**	**<0.001**	**0.004**	0.307	**<0.001**		**<0.001**	0.463	**0.008**	**<0.001**	0.050	0.157
Hymen.	r_s	0.312	**0.608**	**0.631**	**0.663**	0.203	**0.640**	**0.743**		0.383	0.394	**0.667**	-0.232	0.171
	p	0.121	**0.001**	**0.001**	**<0.001**	0.320	**<0.001**	**<0.001**		0.054	0.046	**<0.001**	0.255	0.402
Lepido.	r_s	-0.096	-0.042	0.163	0.179	0.062	0.236	0.151	0.383		0.373	0.162	-0.239	-0.202
	p	0.640	0.838	0.427	0.382	0.763	0.246	0.463	0.054		0.060	0.428	0.240	0.322
Opilio.	r_s	0.326	0.185	0.443	0.427	0.224	0.434	0.506	0.394	0.373		0.641	-0.313	0.01
	p	0.105	0.365	0.023	0.03	0.271	0.027	0.008	0.046	0.060		<0.001	0.119	0.961
Psoco.	r_s	0.481	**0.639**	**0.661**	**0.578**	0.338	**0.727**	**0.774**	**0.667**	0.162	**0.641**		-0.347	**0.517**
	p	0.013	**<0.001**	**<0.001**	**0.002**	0.091	**<0.001**	**<0.001**	**<0.001**	0.428	**<0.001**		0.082	**0.007**
Pulm.	r_s	0.09	0.077	-0.229	-0.170	0.192	-0.314	-0.388	-0.232	-0.239	-0.313	-0.347		-0.004
	p	0.662	0.707	0.261	0.406	0.347	0.119	0.050	0.255	0.240	0.119	0.082		0.984
Thysano.	r_s	0.424	0.382	0.233	0.307	0.235	0.525	0.286	0.171	-0.202	0.01	0.517	-0.004	
	p	0.031	0.054	0.253	0.127	0.249	0.006	0.157	0.402	0.322	0.961	0.007	0.984	

Table C18. Table showing measures of Taxonomic Richness, including five number summary (median, maximum, minimum, first quartile, third quartile) and mean numbers (± SD & ± SE) of canopy-active invertebrate groups collected from both hedge types (Mature hedges, New hedges) during April, July and September 2011

Boundary type	n	Month	Minimu	Media	Maximu	Interquartile range		Mea	±	±
Mature	1	April	4	8	9	7	9	7.62	1.56	0.43
	1	July	6	11	14	10	12.5	11.0	2.09	0.54
	1	Septemb	6	8	14	6	11	8.92	2.84	0.79
New hedge	1	April	4	7	10	7	8	7.54	1.76	0.49
	1	July	7	10	12	9	11	9.88	1.54	0.39
	1	Septemb	5	10	12	7	10	8.77	2.24	0.62

Table C19. Table showing measures of Berger-Parker, including five number summary (median, maximum, minimum, first quartile, third quartile) and mean numbers (± SD & ± SE) of canopy-active invertebrate groups collected from both hedge types (Mature hedges, New hedges) during April, July and September 2011

Boundary type	n	Month	Minimum	Median	Maximum	Interquartile range		Mean	± SD	± SE
Mature hedge	13	April	1.48	2.63	3.78	2.09	3.13	2.61	0.73	0.20
	15	July	1.32	2.73	5.43	2.06	3.93	3.00	1.27	0.33
	16	September	1.55	3.38	4.60	3.12	4.00	3.37	0.95	0.26
New hedge	13	April	1.47	2.05	3.39	1.79	2.80			
	16	July	1.33	2.78	5.50	2.19	3.73	3.02	1.18	0.29
	13	September	1.26	2.35	5.00	2.15	3.95	2.90	1.22	0.34

Table C20. Table showing measures of Shannon, including five number summary (median, maximum, minimum, first quartile, third quartile) and mean numbers (± SD & ± SE) of canopy-active invertebrate groups collected from both hedge types (Mature hedges, New hedges) during April, July and September 2011

Boundary type	n	Month	Minimum	Median	Maximum	Interquartile range		Mean	± SD	± SE
Mature hedge	13	April	1.12	1.55	1.91	1.33	1.70	1.53	0.26	0.07
	15	July	1.06	1.87	2.13	1.54	2.00	1.74	0.34	0.09
	16	September	1.20	1.84	2.03	1.73	1.93	1.79	0.22	0.06
New hedge	13	April	1.15	1.44	1.84	1.34	1.63	1.48	0.22	0.06
	16	July	1.00	1.80	2.53	1.56	1.92	1.75	0.37	0.09
	13	September	0.93	1.57	1.98	1.45	1.88	1.60	0.31	0.09

Table C21. Table showing measures of Simpson, including five number summary (median, maximum, minimum, first quartile, third quartile) and mean numbers (± SD & ± SE) of canopy-active invertebrate groups collected from both hedge types (Mature hedges, New hedges) during April, July and September 2011

Boundary type	n	Month	Minimum	Median	Maximum	Interquartile range		Mean	± SD	± SE
Mature hedge	13	April	2.11	4.09	6.49	2.96	4.83	4.03	1.29	0.36
	15	July	1.71	5.24	8.02	3.61	5.93	4.87	2.01	0.52
	16	September	2.43	5.91	14.00	5.32	7.75	6.71	3.10	0.86
New hedge	13	April	2.05	3.81	5.57	3.00	4.35	3.80	1.10	0.30
	16	July	1.73	4.91	8.49	3.36	6.17	4.83	1.89	0.47
	13	September	1.58	4.74	10.50	3.69	5.75	4.78	2.26	0.63

Table C22. Table showing measures of Heip, including five number summary (median, maximum, minimum, first quartile, third quartile) and mean numbers (± SD & ± SE) of canopy-active invertebrate groups collected from both hedge types (Mature hedges, New hedges) during April, July and September 2011

Boundary type	n	Month	Minimum	Median	Maximum	Interquartile range		Mean	± SD	± SE
Mature hedge	13	April	0.30	0.62	0.82	0.47	0.69	0.58	0.15	0.04
	15	July	0.16	0.53	0.79	0.43	0.64	0.52	0.19	0.05
	16	September	0.38	0.71	0.94	0.51	0.88	0.69	0.20	0.05
New hedge	13	April	0.24	0.58	0.82	0.51	0.60	0.56	0.14	0.04
	16	July	0.16	0.63	1.16	0.44	0.73	0.59	0.23	0.06
	13	September	0.17	0.62	0.87	0.55	0.69	0.57	0.21	0.06

Table C23. Table showing measures of Simpson (evenness), including five number summary (median, maximum, minimum, first quartile, third quartile) and mean numbers (± SD & ± SE) of canopy-active invertebrate groups collected from both hedge types (Mature hedges, New hedges) during April, July and September 2011

Boundary type	n	Month	Minimum	Median	Maximum	Interquartile range		Mean	± SD	± SE
Mature hedge	13	April	0.23	0.59	0.81	0.41	0.64	0.54	0.17	0.05
	15	July	0.13	0.42	0.76	0.36	0.58	0.46	0.20	0.05
	16	September	0.27	0.66	2.33	0.42	1.02	0.86	0.58	0.16
New hedge	13	April	0.20	0.54	1.25	0.41	0.57	0.54	0.25	0.07
	16	July	0.14	0.55	0.77	0.35	0.62	0.50	0.19	0.05
	13	September	0.16	0.53	1.31	0.47	0.69	0.59	0.32	0.09

Table C24. Results of Spearman's *rho* correlations between hedgerow age (years) and canopy-active invertebrate diversity for all months combined and individually (April, July and September) for both Mature and New hedges. Values are r_s plus significance values. Significant values are highlighted in bold. An FDR (Benjamini and Yekuelti) corrected significance level of 0.018 was applied

Diversity measure	All months (n = 83)		April (n = 26)		July (n = 31)		Sept (n = 26)	
	r_s	p	r_s	p	r_s	p	r_s	p
Taxon Richness	0.028	0.799	0.057	0.784	0.319	0.080	-0.087	0.673
Berger-Parker	-0.007	0.952	0.173	0.397	-0.199	0.283	0.031	0.882
Shannon (diversity)	0.026	0.817	0.093	0.651	-0.128	0.492	0.134	0.512
HEIP	-0.067	0.550	0.119	0.561	-0.251	0.173	0.180	0.380
Simpson (diversity)	0.011	0.923	0.040	0.845	-0.157	0.399	0.192	0.346
Simpson (evenness)	-0.002	0.987	0.152	0.458	-0.275	0.134	0.147	0.474

Table C25. Spearman's rank correlations between taxonomic abundance and diversity (Taxon Richness, Berger-Parker, Shannon, Simpson (diversity), Heip, Simpson (evenness)) of the hedge canopy for Mature hedges and New hedges, all months combined (n = 83). B-Y FDR Corrected significance level of 0.010 applies

		Taxon Richness	Berger-Parker	Shannon	Simpson (Diversity)	Heip (Evenness)	Simpson (Evenness)
Collembola	r_s	**0.578**	-0.153	-0.009	-0.214	**-0.381**	**-0.484**
	p	**<0.001**	0.167	0.932	0.052	**<0.001**	**<0.001**
Hemiptera	r_s	**0.676**	0.097	**0.301**	0.059	-0.219	**-0.332**
	p	**<0.001**	0.381	**0.006**	0.598	0.046	**0.002**
Acari	r_s	**0.567**	-0.042	0.137	-0.086	**-0.344**	**-0.398**
	p	**<0.001**	0.705	0.217	0.437	**0.001**	**<0.001**
Araneae	r_s	**0.514**	0.054	0.191	-0.017	**-0.319**	**-0.323**
	p	**<0.001**	0.631	0.083	0.881	**0.003**	**0.003**
Coleoptera	r_s	**0.399**	**-0.283**	-0.179	**-0.393**	**-0.547**	**-0.600**
	p	**<0.001**	**0.010**	0.106	**<0.001**	**<0.001**	**<0.001**
Hymenoptera	r_s	**0.643**	-0.057	0.118	-0.119	**-0.356**	**-0.462**
	p	**<0.001**	0.609	0.287	0.284	**0.001**	**<0.001**
Thysanoptera	r_s	**0.429**	0.002	0.144	-0.012	-0.162	-0.259
	p	**<0.001**	0.985	0.194	0.915	0.143	0.018
Psocoptera	r_s	**0.613**	0.258	**0.435**	**0.284**	-0.052	-0.094
	p	**<0.001**	0.019	**<0.001**	**0.009**	0.638	0.397
Diptera	r_s	**0.487**	-0.114	0.070	-0.158	**-0.445**	**-0.439**
	p	**<0.001**	0.305	0.528	0.155	**<0.001**	**<0.001**
Lepidoptera	r_s	**0.402**	0.029	0.133	-0.003	**-0.291**	-0.210
	p	**<0.001**	0.797	0.232	0.979	**0.008**	0.057
Pulmonata	r_s	**0.311**	0.002	0.124	0.084	-0.108	-0.090
	p	**0.004**	0.989	0.263	0.448	0.330	0.420
Dermaptera	r_s	**0.469**	0.134	0.260	0.133	-0.248	-0.171
	p	**<0.001**	0.226	0.018	0.229	0.024	0.122
Opiliones	r_s	**0.471**	0.129	0.203	0.123	-0.105	-0.118
	p	**<0.001**	0.245	0.066	0.269	0.343	0.290

Table C26. Diversity values for superfamilies/families of Coleoptera and Diptera for Mature Hedges and New Hedges, based on combined totals for: (a) April [n = 13 per hedge type]; (b) July [n = 16]; (c) September [n = 13]

(a)

APRIL	Mature Hedges	New Hedges
Coleoptera		
No. of taxa	12	13
Berger-Parker	2.01	1.74
Shannon	1.32	1.36
Simpson (Diversity)	2.79	2.73
Heip (Evenness)	0.25	0.24
Simpson (Evenness)	0.23	0.21
Diptera		
No. of taxa	5	11
Berger-Parker	1.36	3.70
Shannon	0.89	1.87
Simpson (Diversity)	1.79	5.36
Heip (Evenness)	0.36	0.55
Simpson (Evenness)	0.36	0.49

(b)

JULY	Mature Hedges	New Hedges
Coleoptera		
No. of taxa	10	13
Berger-Parker	2.69	1.74
Shannon	1.57	1.18
Simpson (Diversity)	3.76	2.33
Heip (Evenness)	0.42	0.19
Simpson (Evenness)	0.38	0.18
Diptera		
No. of taxa	12	8
Berger-Parker	2.38	3.11
Shannon	1.87	1.73
Simpson (Diversity)	4.38	5.21
Heip (Evenness)	0.50	0.66
Simpson (Evenness)	0.36	0.65

(c)

SEPTEMBER	Mature Hedges	New Hedges
Coleoptera		
No. of taxa	7	6
Berger-Parker	2.17	3.15
Shannon	1.53	1.54
Simpson (Diversity)	3.59	4.41
Heip (Evenness)	0.60	0.74
Simpson (Evenness)	0.51	0.74
Diptera		
No. of taxa	7	7
Berger-Parker	2.50	3.83
Shannon	1.49	1.84
Simpson (Diversity)	3.90	7.45
Heip (Evenness)	0.57	0.88
Simpson (Evenness)	0.56	1.06

Appendix D. Supplementary information relating to Chapter 6

Table D1. List of names of botanical families (plus Bryophyta), and common family members, found during survey work

Family/Division	Common name
Apiaceae	Carrot Family (notably Cow parsley, Hogweed)
Asteraceae	Daisy Family (Thistles, Burdocks, Mugwort, Ox-eye daisy, Dandelion and other Dandelion-types, Ragworts, Knapweeds and Groundsels)
Boraginaceae	Forget-me-Not Family (including Green Alkanet)
Brassicaceae	Mustard flower Family (notably Jack-in-the-hedge)
Bryophyta	Mosses, liverworts etc
Caryophyllaceae	Pink Family (White and Red Campions)
Chenopodiaceae	Goosefoot Family (notably Fat Hen)
Convolvulaceae	Bindweed Family (Hedge and Field Bindweeds)
Curcurbitaceae	White Bryony
Dennstaediaceae	Bracken Family
Dioscoreaceae	Black Bryony
Fabaceae	Legume/Pea Family (Clovers & Trefoils, Vetches)
Geraniaceae	Geranium Family (various Cranesbill and Herb Robert)
Lamiaceae	Dead nettle Family (notably Ground Ivy, Black Horeshound, Red- and White Dead-nettle)
Onagraceae	Willowherbs
Plantaginaceae	Plantain Family
Polygonaceae	Docks & sorrels (plus Knotgrass, Red Shank)
Poaceae	Grasses
Ranunculaceae	Buttercup Family
Rosaceae	Rose Family (Cinquefoils, Silverweed, Wood Avens)
Rubiaceae	Bedstraw Family (notably Cleavers)
Scrophulariaceae	Speedwells
Urticaceae	Nettle Family (largely Stinging Nettle)

Table D2. Best models ($\Delta i \leq 2$) predicting the abundance of invertebrate taxa in hedgerows at ground level using measures of botanical diversity as explanatory variables. Key to explanatory variables: WTR = Woody taxon richness in the hedgerow itself; MVTRQ = Botanical taxon richness in the margin; TVTR = taxon richness of vegetation in immediate vicinity of trap. Top 10 most abundant taxa shown

Candidate models	k	AICc	Δi	w_i	acc w_i	ER
Collembola						
MVTRQ	2	551.63	0.00	0.20	0.20	---
MVTRQ + TVTR	3	551.66	0.03	0.20	0.40	1.02
WTR + MVTRQ + TVTR	4	551.84	0.21	0.18	0.59	1.11
WTR + MVTRQ	3	552.56	0.93	0.13	0.71	1.59
TVTR	2	552.73	1.10	0.12	0.83	1.73
WTR + TVTR	3	552.76	1.13	0.12	0.94	1.76
Acari						
WTR + MVTRQ + TVTR	4	497.54	0.00	0.48	0.48	---
MVTRQ + TVTR	3	499.06	1.52	0.22	0.70	2.14
WTR + TVTR	3	499.46	1.92	0.18	0.89	2.61
Hemiptera						
TVTR	2	430.73	0.00	0.31	0.31	---
WTR + TVTR	3	431.66	0.93	0.19	0.50	1.59
MVTRQ + TVTR	3	432.56	1.83	0.12	0.62	2.50
Diptera						
WTR	2	372.83	0.00	0.38	0.38	---
WTR + MVTRQ	3	374.76	1.93	0.15	0.53	2.63
Coleoptera						
WTR + TVTR	3	301.96	0.00	0.59	0.59	
WTR + MVTRQ + TVTR	4	303.34	1.38	0.30	0.89	1.99
Hymenoptera						
MVTRQ	2	515.03	0.00	0.17	0.17	---
TVTR	2	515.33	0.30	0.15	0.32	1.16
Intercept	1	515.44	0.41	0.14	0.46	1.23
WTR + TVTR	3	515.56	0.53	0.13	0.59	1.31
WTR + MVTRQ	3	515.66	0.63	0.12	0.71	1.37
MVTRQ + TVTR	3	516.06	1.03	0.10	0.82	1.68
WTR	2	516.23	1.20	0.09	0.91	1.82
WTR+MVTRQ+TVTR	4	516.34	1.31	0.09	1.00	1.93
Thysanoptera						
WTR+MVTRQ+TVTR	4	384.44	0.00	0.42	0.42	---
TVTR	3	384.86	0.42	0.34	0.76	1.23
Opiliones						
Intercept	1	414.40	0.00	0.30	0.30	---
MVTRQ	2	415.20	0.80	0.20	0.50	1.50
TVTR	2	415.90	1.50	0.10	0.60	2.10
WTR	2	416.30	1.90	0.10	0.80	2.60
Araneae						
WTR + MVTRQ	3	262.66	0.00	0.20	0.20	---
WTR	2	263.03	0.37	0.16	0.36	1.20
MVTRQ	2	263.23	0.57	0.15	0.51	1.33

Intercept	1	263.44	0.78	0.13	0.65	1.48
WTR + TVTR	3	263.46	0.80	0.13	0.78	1.49
WTR + MVTRQ + TVTR	4	264.24	1.58	0.09	0.87	2.20
TVTR	2	264.63	1.97	0.07	0.94	2.67
Isopoda						
Intercept	1	260.04	0.00	0.31	0.31	---
WTR + TVTR	3	261.36	1.32	0.16	0.47	1.94
WTR	2	261.43	1.39	0.15	0.62	2.00
MVTRQ	2	261.53	1.49	0.15	0.77	2.10

Table D3. Best models ($\Delta i \leq 2$) predicting abundance of invertebrate taxa in hedgerows at canopy level using measures of botanical diversity as explanatory variables. Top 10 most abundant taxa shown. Explanatory variables: WTR = Woody taxon richness in the hedgerow itself; MVTRQ = Botanical taxon richness in the margin; TVTR = taxon richness of vegetation in immediate vicinity of trap

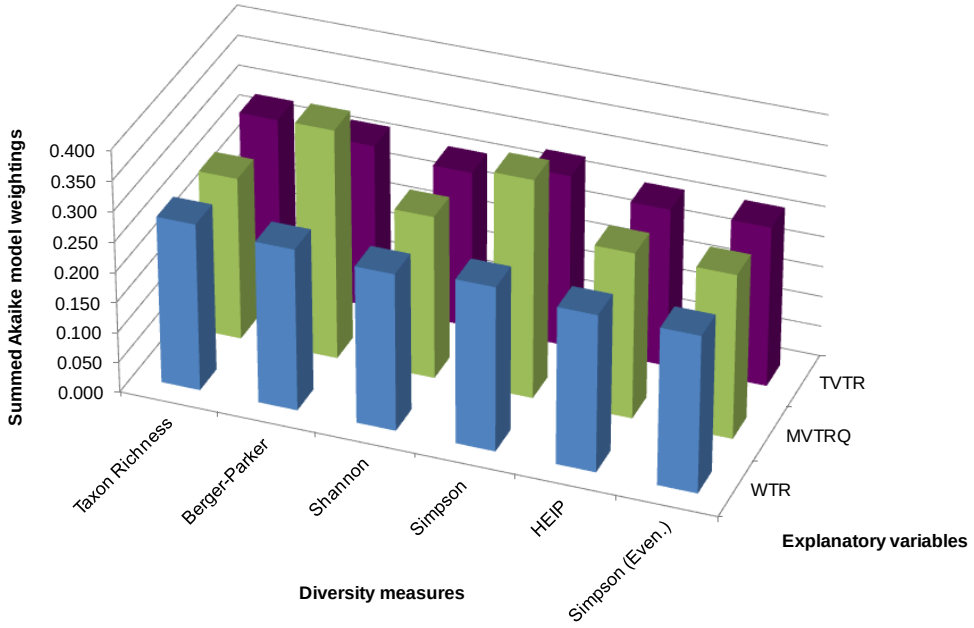
Candidate models	k	AICc	Δi	w_i	acc w_i	ER
Collembola						
Intercept only	1	413.05	0.00	0.21	0.21	---
MVTRQ	2	413.15	0.10	0.20	0.41	1.05
TVTR	2	413.45	0.40	0.17	0.58	1.22
MVTRQ + TVTR	2	414.40	1.35	0.11	0.69	1.97
WTR	3	414.75	1.70	0.09	0.78	2.34
WTR + MVTRQ	3	414.80	1.75	0.09	0.86	2.40
WTR + TVTR	3	414.80	1.75	0.09	0.95	2.40
Acari						
MVTRQ + TVTR	3	294.40	0.00	0.46	0.46	---
WTR + MVTRQ + TVTR	4	295.01	0.61	0.34	0.80	1.36
Hemiptera						
WTR + MVTRQ + TVTR	4	319.41	0.00	0.21	0.21	---
TVTR	2	319.45	0.04	0.21	0.42	1.02
MVTRQ + TVTR	3	319.70	0.29	0.18	0.60	1.16
WTR + TVTR	3	320.10	0.69	0.15	0.75	1.41
WTR	2	320.35	0.94	0.13	0.89	1.60
Diptera						
TVTR	2	209.35	0.00	0.38	0.38	---
Intercept only	1	209.45	0.10	0.36	0.74	1.05
Coleoptera						
Intercept only	1	320.65	0.00	0.26	0.26	---
TVTR	2	320.85	0.20	0.24	0.50	1.11
WTR + TVTR	3	322.30	1.65	0.12	0.62	2.29
WTR	2	322.45	1.80	0.11	0.73	2.46
Hymenoptera						
Intercept only	1	275.55	0.00	0.36	0.36	---
MVTRQ	2	277.15	1.60	0.16	0.52	2.23
TVTR	2	277.35	1.80	0.15	0.67	2.46
WTR	2	277.55	2.00	0.13	0.80	2.72
Thysanoptera						
MVTRQ + TVTR	3	245.10	0.00	0.65	0.65	---
Psocoptera						
Intercept only	1	252.75	0.00	0.36	0.36	---

	MVTRQ	2	254.05	1.30	0.19	0.54	1.92
Araneae							
	Intercept only	1	261.65	0.00	0.28	0.28	---
	WTR	2	262.25	0.60	0.21	0.49	1.35
	MVTRQ	2	262.95	1.30	0.15	0.64	1.92
	WTR + MVTRQ	3	263.60	1.95	0.11	0.74	2.66
Lepidoptera							
	TVTR	2	133.05	0.00	0.54	0.54	---

Table D4. Spearman rank correlations between TVTR (vegetation diversity at trap site) and canopy-active invertebrate abundance. Top 10 most abundant tax only shown. Significant relationships are highlighted in bold and shaded in green. An FDR-corrected significance level of 0.017 was applied

Taxa	n	r_s	*p*
Total Abundance (all taxa)	83	0.188	0.089
Collembola	83	0.102	0.360
Hemiptera	83	0.226	0.040
Acari	83	**0.322**	**0.003**
Araneae	83	-0.004	0.972
Coleoptera	83	0.110	0.322
Hymenoptera	83	0.052	0.639
Thysanoptera	83	**0.352**	**0.001**
Psocoptera	83	-0.016	0.885
Diptera	83	0.124	0.263
Lepidoptera	83	**0.338**	**0.002**

(a)



(b)

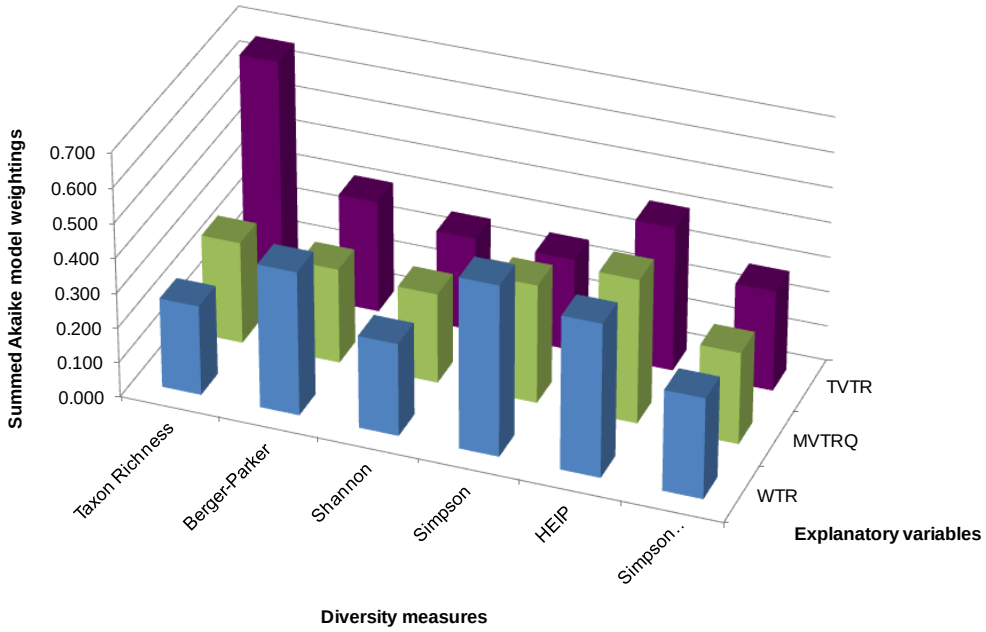


Figure D1. Summed candidate Akaike model weights for botanical diversity variables potentially explaining measures of invertebrate diversity at: (a) ground level, and (b) canopy level. Explanatory variables: WTR = Woody taxon richness in the hedgerow itself; MVTRQ = Botanical taxon richness in the margin measured by quadrat; TVTR = taxon richness of vegetation in immediate vicinity of trap

Table D5. Best models (Δi ≤ 2) predicting abundance of invertebrate taxa in hedgerows at ground level using measures of vegetation structure as explanatory variables. Top 10 most abundant taxa only shown. Variables: CQ = ground cover as measured within 2 x 1m quadrats; GL = light conditions, measured in Lux, at ground level; MSH = maximum sward height; MW = margin width

Candidate models	k	AICc	Δi	w_i	acc w_i	ER
Collembola						
MSH + MW	3	552.46	0.00	0.16	0.16	---
MSH + GL + MW	4	552.84	0.38	0.13	0.29	1.21
CQ + MSH + MW	4	553.34	0.88	0.10	0.39	1.55
MW	2	553.73	1.27	0.08	0.47	1.88
MSH + GL	3	554.06	1.60	0.07	0.54	2.23
MSH	2	554.23	1.77	0.07	0.61	2.42
CQ + MSH	3	554.36	1.90	0.06	0.67	2.59
Acari						
CQ + MSH + GL	4	499.54	0.00	0.28	0.28	---
MSH + GL + MW	3	500.26	0.72	0.19	0.47	1.43
CQ + MSH + GL + MW	5	500.47	0.93	0.17	0.64	1.59
MSH + GL + MW	4	500.54	1.00	0.17	0.81	1.65
Hemiptera						
CQ + MSH	3	393.46	0.00	0.38	0.38	---
CQ + MSH + MW	4	395.24	1.78	0.16	0.53	2.44
Diptera						
CQ + MSH + MW	4	364.74	0.00	0.27	0.27	---
CQ + MW	3	365.36	0.62	0.20	0.46	1.36
CQ + MSH	3	366.26	1.52	0.12	0.59	2.14
CQ + MSH + GL + MW	5	366.57	1.83	0.11	0.69	2.50
Coleoptera						
GL	2	309.53	0.00	0.14	0.14	---
CQ	2	310.13	0.60	0.11	0.25	1.35
CQ + GL	3	310.16	0.63	0.11	0.36	1.37
GL + MW	3	310.36	0.83	0.10	0.45	1.52
CQ + GL + MW	4	310.54	1.01	0.09	0.54	1.66
CQ + MW	3	310.66	1.13	0.08	0.62	1.76
Intercept	1	311.14	1.61	0.06	0.69	2.24
MSH + GL	3	311.36	1.83	0.06	0.74	2.50
Hymenoptera						
MSH + GL	3	492.06	0.00	0.35	0.35	---
CQ + MSH + MW	4	493.14	1.08	0.20	0.55	1.72
GL	4	493.54	1.48	0.17	0.71	2.10
Thysanoptera						
MSH + GL	3	381.16	0.00	0.54	0.54	---
Opiliones						
CQ + MSH	3	401.06	0.00	0.41	0.41	---
CQ + MSH + MW	4	402.14	1.08	0.24	0.65	1.72
CQ + MSH + GL	4	402.74	1.68	0.18	0.83	2.32
Araneae						
CQ + MSH + MW	4	261.94	0.00	0.15	0.15	---
CQ + MSH	3	262.26	0.32	0.13	0.27	1.17
CQ + MW	3	262.26	0.32	0.13	0.40	1.17
CQ	2	262.53	0.59	0.11	0.51	1.34
Intercept	1	263.44	1.50	0.07	0.58	2.12
MSH	2	263.73	1.79	0.06	0.64	2.44

Isopoda						
CQ + MSH	3	256.46	0.00	0.22	0.22	---
MSH	2	256.73	0.27	0.20	0.42	1.14
CQ + MSH + MW	4	258.44	1.98	0.08	0.50	2.69

Table D6. Best models (Δi ≤ 2) predicting abundance of invertebrate taxa in hedgerows at canopy level using measures of vegetation structure as explanatory variables. Top 10 most abundant taxa only shown. Variables: CQ = ground cover as measured within 2 x 1m quadrats; GL = light conditions, measured in Lux, at ground level; MSH = maximum sward height; MW = margin width

Candidate models	k	AICc	Δi	w_i	acc w_i	ER
Collembola						
GL	2	396.05	0.00	0.38	0.38	---
GL + MW	3	397.70	1.65	0.17	0.55	2.29
MSH + GL	3	398.00	1.95	0.14	0.69	2.66
Acari						
GL	2	299.55	0.00	0.19	0.19	---
MSH + GL	3	299.60	0.05	0.18	0.37	1.03
GL + MW	3	299.90	0.35	0.16	0.53	1.19
MSH + GL + MW	4	300.01	0.46	0.15	0.68	1.26
CQ + GL	3	300.90	1.35	0.10	0.77	1.97
CQ + MSM + GL	4	301.11	1.56	0.09	0.86	2.18
Hemiptera						
MSH + GL	3	304.90	0.00	0.48	0.48	---
Diptera						
CQ + GL	3	207.40	0.00	0.22	0.22	---
GL	2	208.05	0.65	0.16	0.39	1.38
CQ	2	208.45	1.05	0.13	0.52	1.69
Coleoptera						
GL + MW	3	317.30	0.00	0.18	0.18	---
GL	2	317.55	0.25	0.16	0.34	1.13
MSH + GL + MW	4	317.81	0.51	0.14	0.48	1.29
MSM + GL	3	318.20	0.90	0.12	0.60	1.57
Hymenoptera						
GL	2	265.55	0.00	0.33	0.33	---
GL + MW	3	266.40	0.85	0.21	0.54	1.53
Thysanoptera						
CQ + MSH + GL	4	238.81	0.00	0.48	0.48	---
MSH + GL	3	240.60	1.79	0.20	0.68	2.45
Psocoptera						
MSH	2	246.05	0.00	0.20	0.20	---
MSH + GL	3	246.10	0.05	0.20	0.40	1.03
MSH + GL + MW	4	246.41	0.36	0.17	0.57	1.20
MSH + MW	3	246.80	0.75	0.14	0.71	1.46
Araneae						
GL	2	259.35	0.00	0.22	0.22	---
CQ + GL	3	259.50	0.15	0.21	0.43	1.08
Lepidoptera						
Intercept only	1	140.75	0.00	0.21	0.21	---
CQ	2	142.05	1.30	0.11	0.32	1.92
MSM	2	142.05	1.30	0.11	0.43	1.92

MW	2	142.25	1.50	0.10	0.52	2.12
GL	2	142.35	1.60	0.09	0.62	2.23

Table D7. Best models ($\Delta i \leq 2$) explaining the abundance of invertebrate taxa in hedgerows at ground level using measures of hedge structure as explanatory variables. Ten most abundant taxa only shown. Explanatory variables: CL = Canopy light penetration; COA = Canopy width; HA = Height; HAA = Height of canopy above ground; HG = Height growth; WG = Width growth

Candidate models	k	AICc	Δi	w_i	acc w_i	ER
Collembola						
COA + HAA + CL	4	548.94	0.00	0.12	0.12	---
COA + CL	3	550.16	1.22	0.07	0.19	1.84
HAA + CL	3	550.16	1.22	0.07	0.25	1.84
COA + WG + HAA + CL	5	550.17	1.23	0.07	0.32	1.85
HA + HAA + CL	4	550.74	1.80	0.05	0.37	2.46
HG + HA + CL	4	550.74	1.80	0.05	0.42	2.46
HG + HAA	3	550.86	1.92	0.05	0.46	2.61
HG + COA + HAA + CL	5	550.87	1.93	0.05	0.51	2.62
HAA	2	550.93	1.99	0.05	0.56	2.70
Acari						
HG + CL	3	506.96	0.00	0.10	0.10	---
HG + COA + CL	4	507.64	0.68	0.07	0.18	1.41
CL	2	508.13	1.17	0.06	0.24	1.79
HA + HG + CL	4	508.14	1.18	0.06	0.29	1.80
HG + HAA + CL	4	508.24	1.28	0.06	0.35	1.90
HG + COA + HAA + CL	5	508.57	1.61	0.05	0.40	2.24
Hemiptera						
COA + HAA + CL	4	425.64	0.00	0.13	0.13	---
HG + COA + HAA + CL	5	426.37	0.73	0.09	0.22	1.44
HA + HAA + CL	4	426.94	1.30	0.07	0.28	1.92
COA + WG + HAA + CL	5	426.97	1.33	0.07	0.35	1.94
HA + WG + HAA + CL	5	427.57	1.93	0.05	0.40	2.62
WG + HA + CL	4	427.64	2.00	0.05	0.44	2.72
Diptera						
COA	2	363.83	0.00	0.12	0.12	---
HA	2	365.03	1.20	0.07	0.19	1.82
COA + CL	3	365.26	1.43	0.06	0.25	2.05
HA + COA	3	365.36	1.53	0.06	0.30	2.15
HG + COA	3	365.66	1.83	0.05	0.35	2.50
Coleoptera						
HA	2	303.83	0.00	0.15	0.15	---
HA + HAA	3	305.36	1.53	0.07	0.22	2.15
HA + HG	3	305.46	1.63	0.07	0.29	2.26
Hymenoptera						
CL	2	504.13	0.00	0.16	0.16	---
HG + CL	3	505.26	1.13	0.09	0.26	1.76
HA + CL	3	505.96	1.83	0.07	0.32	2.50
HAA + CL	3	506.06	1.93	0.06	0.39	2.63
Thysanoptera						
HG + CL	3	392.26	0.00	0.10	0.10	---
HA + CL	3	392.66	0.40	0.08	0.18	1.22

CL	2	392.83	0.57	0.07	0.26	1.33
HA + HG + CL	4	393.34	1.08	0.06	0.31	1.72
HG + HAA + CL	4	393.64	1.38	0.05	0.36	1.99
HG + WG	4	394.04	1.78	0.04	0.40	2.44
COA	3	394.26	2.00	0.04	0.44	2.72
Opiliones						
HA + HG + HAA + CL	5	399.87	0.00	0.26	0.26	---
HA + HAA + CL	4	400.94	1.07	0.15	0.42	1.71
HA + HG + WG + HAA + CL	6	401.35	1.48	0.13	0.54	2.10
Araneae						
HA + HAA	3	260.16	0.00	0.10	0.10	---
HA + HG + HAA	4	261.04	0.88	0.06	0.16	1.55
HAA	2	261.13	0.97	0.06	0.22	1.62
HA + COA + HAA	4	261.64	1.48	0.05	0.27	2.10
HA + WG + HAA	4	261.94	1.78	0.04	0.31	2.44
HA	2	262.13	1.97	0.04	0.34	2.67
COA + HAA	3	262.16	2.00	0.04	0.38	2.72
Isopoda						
HG + CL	3	250.76	0.00	0.16	0.16	---
HG + HAA + CL	4	251.94	1.18	0.09	0.25	1.80
HAA + CL	3	252.46	1.70	0.07	0.32	2.34
HG + WG + CL	4	252.54	1.78	0.07	0.39	2.44

Table D8. Spearman rank correlations between invertebrate abundance (all taxa summed and top ten individual taxa) at ground level and CL (canopy light levels). All months combined. Significant results highlighted in bold and shaded. An FDR-corrected significance level of 0.017 was applied

Taxa	n	r_s	*p*
Total Abundance (all taxa)	95	-0.176	0.088
Collembola	95	0.083	0.425
Acari	95	-0.242	0.018
Hemiptera	95	-0.232	0.024
Diptera	95	-0.128	0.217
Coleoptera	95	-0.125	0.227
Hymenoptera	95	**-0.351**	**<0.001**
Thysanoptera	95	**-0.369**	**<0.001**
Opiliones	95	-0.160	0.121
Araneae	95	-0.020	0.851
Isopoda	95	-0.202	0.050

Table D9. Spearman rank correlations between invertebrate abundance (all taxa summed and top ten individual taxa) at ground level and HG (Growth of Height of Canopy). All months combined. An FDR-corrected significance level of 0.017 was applied

Taxa	n	r_s	*p*
Total Abundance (all taxa)	95	-0.162	0.120
Collembola	95	-0.050	0.631
Acari	95	-0.175	0.090
Hemiptera	95	-0.050	0.632
Diptera	95	-0.048	0.647
Coleoptera	95	-0.081	0.437
Hymenoptera	95	-0.065	0.534
Thysanoptera	95	-0.080	0.441
Opiliones	95	-0.124	0.230
Araneae	95	-0.026	0.805
Isopoda	95	-0.117	0.258

Table D10. Spearman rank correlations between invertebrate abundance (all taxa summed and top ten individual taxa) at ground level and HAA (Height of Canopy Above Ground). All months combined. An FDR-corrected significance level of 0.017 was applied

Taxa	n	r_s	*p*
Total Abundance (all taxa)	95	-0.071	0.49
Collembola	95	-0.144	0.163
Acari	95	0.012	0.906
Hemiptera	95	0.206	0.046
Diptera	95	0.047	0.652
Coleoptera	95	0.038	0.713
Hymenoptera	95	-0.082	0.430
Thysanoptera	95	0.010	0.923
Opiliones	95	0.237	0.021
Araneae	95	-0.122	0.238
Isopoda	95	0.107	0.304

Table D11. Best models ($\Delta i \leq 2$) explaining the abundance of invertebrate taxa in hedgerows at canopy level using measures of hedge structure as explanatory variables. Top 10 most abundant taxa only. Explanatory variables: CL = Canopy light penetration; COA = Canopy width; HA = Height; HAA = Height of canopy above ground; HG = Height growth; WG = Width growth

Candidate models	k	AICc	Δi	w_i	acc w_i	ER
Collembola						
HA + HAA + CL	4	403.31	0.00	0.09	0.09	---
HA + HAA	3	403.50	0.19	0.08	0.18	1.10
COA + HAA + CL	4	403.91	0.60	0.07	0.25	1.35
COA + HAA	3	404.30	0.99	0.06	0.30	1.64
HAA + CL	3	404.40	1.09	0.05	0.36	1.73
HA + HG + HAA	4	404.81	1.50	0.04	0.40	2.12
HG + COA + HAA	4	404.81	1.50	0.04	0.44	2.12
HA + HG + HAA + CL	5	405.08	1.77	0.04	0.48	2.42
HG + COA + HAA + CL	5	405.18	1.87	0.04	0.52	2.54
Acari						
HA	2	306.85	0.00	0.07	0.07	---
HA + CL	3	307.70	0.85	0.04	0.11	1.53
HA + HAA	3	307.80	0.95	0.04	0.16	1.61
HAA + CL	3	307.80	0.95	0.04	0.20	1.61
HA + HG + HAA	4	307.91	1.06	0.04	0.24	1.70
HA + COA	3	308.00	1.15	0.04	0.28	1.78
HA + HAA + CL	4	308.01	1.16	0.04	0.32	1.79
CL	2	308.25	1.40	0.03	0.35	2.01
HA + HG	3	308.40	1.55	0.03	0.38	2.17
HA + COA + CL	4	308.51	1.66	0.03	0.41	2.30
Intercept	1	308.65	1.80	0.03	0.44	2.46
HA + HG + HAA + CL	5	308.68	1.83	0.03	0.47	2.50
Hemiptera						
HG + COA + WG + HAA + CL	6	304.81	0.00	0.27	0.27	---
HG + COA + HAA + CL	5	306.18	1.37	0.14	0.41	1.99
HA + HG + HAA + CL	5	306.78	1.97	0.10	0.51	2.68
Diptera						
HA + HG	3	203.20	0.00	0.18	0.18	---
HA + HG + CL	4	205.01	1.81	0.07	0.25	2.47
Coleoptera						
HG + COA	3	317.00	0.00	0.10	0.10	---
HA + HG	3	318.50	1.50	0.05	0.14	2.12
HG + COA + CL	4	318.51	1.51	0.05	0.19	2.13
COA	2	318.55	1.55	0.05	0.24	2.17
HA	2	318.95	1.95	0.04	0.27	2.65
COA + CL	3	319.00	2.00	0.04	0.31	2.72
Hymenoptera						
CL	2	268.15	0.00	0.12	0.12	---
HA + CL	3	268.60	0.45	0.10	0.22	1.25
WG + CL	3	269.80	1.65	0.05	0.27	2.29
COA + CL	3	269.90	1.75	0.05	0.32	2.40
HAA + CL	3	270.00	1.85	0.05	0.36	2.53
HA + HG + CL	4	270.01	1.86	0.05	0.41	2.54
HA + HAA + CL	4	270.11	1.96	0.04	0.46	2.67
Thysanoptera						
HAA + CL	3	259.10	0.00	0.06	0.06	---

HA + HAA + CL	4	259.21	0.11	0.05	0.11	1.06
Intercept	1	259.55	0.45	0.04	0.15	1.25
HAA	2	259.55	0.45	0.04	0.20	1.25
HA + HG + CL	4	259.81	0.71	0.04	0.24	1.43
HG + COA + CL	4	259.91	0.81	0.04	0.28	1.50
CL	2	259.95	0.85	0.04	0.31	1.53
COA + HAA + CL	4	260.11	1.01	0.03	0.35	1.66
HA + HG + HAA + CL	5	260.38	1.28	0.03	0.38	1.89
HG + CL	3	260.40	1.30	0.03	0.41	1.92
HG	2	260.55	1.45	0.03	0.43	2.06
HA + CL	3	260.70	1.60	0.03	0.46	2.23
HG + HAA + CL	4	260.91	1.81	0.02	0.48	2.47
HG + COA + HAA + CL	5	260.98	1.88	0.02	0.50	2.55
HA + HAA	3	261.00	1.90	0.02	0.53	2.59
COA + CL	3	261.10	2.00	0.02	0.55	2.72
Psocoptera						
HAA + CL	3	237.70	0.00	0.11	0.11	---
CL	2	237.75	0.05	0.11	0.22	1.02
WG + CL	3	238.60	0.90	0.07	0.29	1.57
COA + HAA + CL	4	238.61	0.91	0.07	0.36	1.58
COA + CL	3	239.00	1.30	0.06	0.41	1.92
HA + HAA + CL	4	239.01	1.31	0.06	0.47	1.92
HA + CL	3	239.50	1.80	0.04	0.51	2.46
HG + CL	3	239.50	1.80	0.04	0.56	2.46
WG + HAA + CL	4	239.51	1.81	0.04	0.60	2.47
Araneae						
HG + CL	3	254.20	0.00	0.14	0.14	---
HA + HG + CL	4	254.61	0.41	0.12	0.26	1.23
HG + COA + CL	4	255.61	1.41	0.07	0.33	2.02
HG	2	256.05	1.85	0.06	0.38	2.52
Lepidoptera						
HA	2	135.65	0.00	0.13	0.13	---
COA	2	136.55	0.90	0.08	0.22	1.57
HA + COA	3	137.50	1.85	0.05	0.27	2.53
HA + CL	3	137.50	1.85	0.05	0.32	2.53

Table D12. Spearman rank correlations between HA (Height) and canopy-active invertebrate abundance. Top 10 most abundant tax only shown. Significant relationships are highlighted in bold and shaded in green. An FDR-corrected significance level of 0.017 was applied

Taxa	n	r_s	*p*
Total Abundance (all taxa)	83	0.167	0.131
Collembola	83	0.154	0.166
Hemiptera	**83**	**0.345**	**0.001**
Acari	83	0.145	0.190
Araneae	83	-0.169	0.128
Coleoptera	83	0.086	0.442
Hymenoptera	83	0.167	0.131
Thysanoptera	83	0.006	0.960
Psocoptera	83	0.207	0.061
Diptera	83	0.200	0.070
Lepidoptera	**83**	**0.283**	**0.009**

Table D13. Spearman rank correlations between COA (Canopy width) and canopy-active invertebrate abundance. Top 10 most abundant tax only shown. Significant relationships are highlighted in bold and shaded in green. An FDR-corrected significance level of 0.017 was applied

Taxa	n	r_s	*p*
Total Abundance (all taxa)	83	0.169	0.127
Collembola	83	0.177	0.108
Hemiptera	83	0.226	0.040
Acari	83	0.094	0.400
Araneae	83	-0.179	0.105
Coleoptera	83	0.134	0.229
Hymenoptera	83	0.091	0.411
Thysanoptera	83	-0.024	0.828
Psocoptera	83	0.157	0.156
Diptera	83	0.157	0.155
Lepidoptera	**83**	**0.295**	**0.007**

Table D14. Spearman rank correlations between HG (Height growth) and canopy-active invertebrate abundance. Top 10 most abundant taxa only shown. Significant relationships are highlighted in bold. An FDR-corrected significance level of 0.017 was applied

Taxa	n	r_s	*p*
Total Abundance (all taxa)	83	0.230	0.037
Collembola	83	0.154	0.164
Hemiptera	83	0.196	0.075
Acari	83	0.034	0.759
Araneae	**83**	**0.442**	**<0.001**
Coleoptera	83	0.149	0.180
Hymenoptera	83	0.170	0.125
Thysanoptera	83	-0.117	0.294
Psocoptera	83	0.053	0.634
Diptera	83	0.186	0.092
Lepidoptera	83	0.049	0.657

Table D15. Spearman rank correlations between measures of invertebrate diversity in the hedge bottom and HAA (Height above ground). An FDR-corrected significance level of 0.017 was applied

Taxa	n	r_s	*p*
TaxonRichness	95	-0.071	0.493
Berger-Parker	95	-0.144	0.163
Shannon	95	0.012	0.906
Simpson (diversity)	95	0.206	0.046
Heip (evenness)	95	0.047	0.652
Simpson (evenness)	95	0.038	0.713

Table D16. Best models (Δi ≤ 2) explaining the abundance of invertebrate taxa in hedgerows at ground level using measures of landscape context as explanatory variables. Top 10 most abundant taxa only. Key to variables: C = connectivity, *i.e.* number of connections with other hedgerows; DW = distance from woodland; L = location

Candidate models	k	AICc	Δi	w_i	acc w_i	ER
Collembola						
DW	2	551.03	0.00	0.30	0.30	---
L	2	551.23	0.20	0.27	0.58	1.11
DW & C	3	552.96	1.93	0.12	0.69	2.63
Acari						
DW & L	3	506.76	0.00	0.29	0.29	---
L	2	507.03	0.27	0.26	0.55	1.14
DW & L & C	4	508.54	1.78	0.12	0.67	2.44
Hemiptera						
L	2	432.73	0.00	0.22	0.22	---
Intercept	1	432.74	0.01	0.22	0.44	1.01
C	2	433.03	0.30	0.19	0.64	1.16
DW	2	434.43	1.70	0.10	0.73	2.34
L & C	3	434.56	1.83	0.09	0.82	2.50
Diptera						---
DW & L	3	362.36	0.00	0.48	0.48	---
L	2	363.63	1.27	0.25	0.73	1.88
Coleoptera						
DW & L	3	298.16	0.00	0.40	0.40	---
L	2	298.53	0.37	0.33	0.74	1.20
Hymenoptera						
Intercept	1	515.44	0.00	0.43	0.43	---
DW	2	517.43	1.99	0.16	0.58	2.70
C	2	517.43	1.99	0.16	0.74	2.70
Thysanoptera						
L	2	397.83	0.00	0.36	0.36	---
L & C	3	399.76	1.93	0.14	0.50	2.63
DW	2	399.83	2.00	0.13	0.63	2.72
Opiliones						
L	2	412.33	0.00	0.23	0.23	---
C	2	413.03	0.70	0.17	0.40	1.42
DW & L	3	413.36	1.03	0.14	0.54	1.68
L & C	3	413.76	1.43	0.11	0.66	2.05
DW	2	414.03	1.70	0.10	0.76	2.34
DW & C	3	414.06	1.73	0.10	0.85	2.38
Araneae						
Intercept	1	263.44	0.00	0.42	0.42	---
DW	2	265.23	1.79	0.17	0.59	2.44
C	2	265.23	1.79	0.17	0.76	2.44
Isopoda						
L	2	257.73	0.00	0.37	0.37	---
L & C	3	259.46	1.73	0.15	0.52	2.38
DW & L	3	259.86	2.13	0.13	0.65	2.91

Table D17. Results of Spearman rank correlations between DW (Distance from Woodland) and abundance of hedge bottom invertebrates. All hedges and all months combined (April,

July, September). Significant relationships are highlighted in bold and shaded. A Benjamini – Yekultieli method FDR corrected significance level of 0.017 applies

Taxa	n	r_s	*p*
Total Abundance (all taxa)	95	0.007	0.948
Collembola	95	-0.174	0.093
Acari	95	0.154	0.135
Hemiptera	95	0.030	0.770
Diptera	95	-0.173	0.093
Coleoptera	95	-0.063	0.544
Hymenoptera	95	0.040	0.699
Thysanoptera	95	-0.027	0.792
Opiliones	95	0.210	0.042
Araneae	95	-0.025	0.813
Isopoda	95	0.040	0.699

Table D18. Best models (Δi ≤ 2) explaining the abundance of invertebrate taxa in hedgerows at canopy level using measures of landscape context as explanatory variables. Top 10 most abundant taxa only. Key to variables: C = connectivity, *i.e.* number of connections with other hedgerows; DW = distance from woodland; L = location

Candidate models	k	AICc	Δ*i*	w_i	acc w_i	ER
Collembola						
DW	2	465.35	0.00	0.38	0.38	---
Intercept	1	466.45	1.10	0.22	0.60	1.73
Acari						
Intercept	1	308.65	0.00	0.28	0.28	---
L	2	309.45	0.80	0.19	0.47	1.49
C	2	309.95	1.30	0.15	0.62	1.92
L + C	3	310.60	1.95	0.11	0.72	2.66
Hemiptera						
L	2	321.75	0.00	0.34	0.34	---
Intercept	1	323.35	1.60	0.15	0.49	2.22
L + C	3	323.70	1.95	0.13	0.62	2.66
DW	2	323.75	2.00	0.12	0.74	2.72
Diptera						
Intercept	1	211.45	0.00	0.25	0.25	---
DW	2	211.75	0.30	0.21	0.46	1.16
L + C	2	212.75	1.30	0.13	0.58	1.92
DW + C	3	212.90	1.45	0.12	0.70	2.07
C	2	212.95	1.50	0.12	0.82	2.12
L + C	3	213.30	1.85	0.10	0.92	2.53
Coleoptera						
Intercept	1	320.65	0.00	0.36	0.36	---
DW	2	321.95	1.30	0.19	0.54	1.92
Hymenoptera						
DW	2	275.25	0.00	0.33	0.33	---
Intercept	1	275.55	0.30	0.28	0.61	1.16
Thysanoptera						
Intercept	1	259.55	0.00	0.35	0.35	---
C	2	259.95	0.40	0.29	0.64	1.22
DW	2	261.15	1.60	0.16	0.80	2.23
Psocoptera						
DW	2	252.55	0.00	0.28	0.28	---
Intercept	1	252.75	0.20	0.26	0.54	1.10
DW + C	3	254.20	1.65	0.12	0.66	2.29
C	2	254.35	1.80	0.11	0.78	2.46
Araneae						
L	2	253.45	0.00	0.47	0.47	---
DW + L	3	255.00	1.55	0.22	0.69	2.17
L + C	3	255.10	1.65	0.21	0.89	2.29
Lepidoptera						
L	2	139.95	0.00	0.27	0.27	---
Intercept	1	140.75	0.80	0.18	0.45	1.49
DW	2	141.05	1.10	0.16	0.61	1.73
L + C	3	141.60	1.65	0.12	0.73	2.29

Table D19. Spearman rank correlations between DW (Distance from woodland) and measures of invertebrate diversity in the hedge bottom. All hedges and all months combined (April, July, September)

Measure of diversity	n	r_s	*p*
Taxon Richness	95	0.028	0.786
Berger-Parker	95	0.037	0.725
Shannon	95	0.030	0.773
Simpson (Diversity)	95	0.023	0.828
HEIP (Evenness)	95	0.009	0.932
Simpson (Evenness)	95	0.013	0.900

Table D20. Spearman rank correlations between C (Connectivity) and measures of invertebrate diversity in the hedge bottom. All hedges and all months combined (April, July, September)

Measure of diversity	n	r_s	*p*
Taxon Richness	95	0.163	0.114
Berger-Parker	95	0.097	0.351
Shannon	95	0.125	0.226
Simpson (Diversity)	95	0.114	0.272
HEIP (Evenness)	95	0.022	0.832
Simpson (Evenness)	95	0.046	0.659

Table D21. Best models (Δi ≤ 2) explaining the abundance of invertebrate taxa in hedgerows at ground level using weather conditions (www.wunderground.com) as explanatory variables. Key to weather variables: H = humidity; R = rain; T = temperature; W = wind speed

Candidate models	k	AICc	Δi	w_i	acc w_i	ER
Collembola						
T + W + R	3	532.14	0.00	0.66	0.66	---
T + H + W + R	5	533.77	1.63	0.29	0.95	2.26
Acari						
W + R	3	455.76	0.00	0.42	0.42	---
T + W + R	4	456.44	0.68	0.30	0.72	1.41
H + W + R	4	457.74	1.98	0.16	0.88	2.69
Hemiptera						
T + W + R	4	402.84	0.00	0.53	0.53	---
Diptera						
T + H + R	4	365.04	0.00	0.23	0.23	---
T + R	3	365.26	0.22	0.21	0.45	1.12
T + H	3	365.96	0.92	0.15	0.59	1.58
T + W + R	4	366.84	1.80	0.10	0.69	2.46
Coleoptera						
W + R	3	284.76	0.00	0.52	0.52	---
H + W + R	4	286.64	1.88	0.20	0.73	2.56
T + W + R	4	286.74	1.98	0.19	0.92	2.69
Hymenoptera						
T + H + R	4	474.84	0.00	0.70	0.70	---
Thysanoptera						
T + W + R	4	347.44	0.00	0.50	0.50	---
W + R	3	348.96	1.52	0.23	0.73	2.14
Opiliones						
T + H + R	4	371.14	0.00	0.59	0.59	---
T + H + W + R	5	372.47	1.33	0.30	0.90	1.94
Araneae						
R	2	255.53	0.00	0.35	0.35	---
T + R	3	256.96	1.43	0.17	0.53	2.05
H + R	3	257.36	1.83	0.14	0.67	2.50
Isopoda						
T + R	3	246.16	0.00	0.32	0.32	---
T + H + R	4	246.64	0.48	0.26	0.58	1.27

Table D22. Best models (Δi ≤ 2) explaining the abundance of invertebrate taxa in hedgerows at canopy level using weather conditions (Silva handheld weather station) as explanatory variables. Key to weather variables: HH = humidity handheld; TH = temperature handheld; WSH = wind speed handheld. Rainfall was not included since beatings were only conducted in dry conditions

Candidate models	k	AICc	Δi	w_i	acc w_i	ER
Collembola						
HH + WSH	3	396.00	0.00	0.45	0.45	---
TH + WSH	3	396.20	0.20	0.40	0.85	1.11
Acari						
WSH	2	301.05	0.00	0.41	0.41	---
TH + WSH	3	301.90	0.85	0.27	0.67	1.53
HH + WSH	3	302.40	1.35	0.21	0.88	1.97
Hemiptera						
Intercept	1	323.35	0.00	0.17	0.17	---
TH	2	323.35	0.00	0.17	0.33	1.00
HH	2	323.35	0.00	0.17	0.50	1.00
WSH	2	323.55	0.20	0.15	0.65	1.11
TH + WSH	3	323.70	0.35	0.14	0.79	1.19
HH + WSH	3	324.40	1.05	0.10	0.88	1.69
TH + HH	3	325.10	1.75	0.07	0.95	2.40
Diptera						
TH + HH + WSH	4	203.01	0.00	0.45	0.45	---
WSH	2	204.15	1.14	0.26	0.71	1.77
Coleoptera						
TH + HH + WSH	4	303.41	0.00	0.60	0.60	---
TH + WSH	3	304.30	0.89	0.38	0.98	1.56
Hymenoptera						
TH + WSH	3	271.10	0.00	0.36	0.36	---
Thysanoptera						
Intercept	1	259.55	0.00	0.32	0.32	---
WSH	2	260.25	0.70	0.22	0.54	1.42
HH	2	261.45	1.90	0.12	0.67	2.59
Psocoptera						
TH + WSH	3	245.80	0.00	0.36	0.36	---
TH + HH + WSH	4	246.11	0.31	0.31	0.67	1.17
WSH	2	247.15	1.35	0.18	0.85	1.96
Araneae						
Intercept	1	261.65	0.00	0.28	0.28	---
WSH	2	262.35	0.70	0.20	0.48	1.42
TH	2	262.95	1.30	0.15	0.63	1.92
HH	2	263.65	2.00	0.10	0.73	2.72
Lepidoptera						
TH	2	142.25	0.00	0.25	0.25	---
WSH	2	142.65	0.40	0.21	0.46	1.22
HH	2	142.85	0.60	0.19	0.65	1.35
T& H	3	144.00	1.75	0.11	0.75	2.40
T + WS	3	144.20	1.95	0.10	0.85	2.66